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EXPERIMENTAL INDUCTION OF FLOWER FORMATION IN KIKUYU GRASS (*PENNISETUM CLANDESTINUM* HOCHST. EX CHIOV.)

By D. J. Carr* and Eng Kok Ng*

(*Manuscript received August* 2, 1955)

Summary

The literature on the flowering of kikuyu grass (*Pennisetum clandestinum* Hochst. ex Chiov.) is summarized. It is shown to be probable that some very vigorous strains are genetically male-sterile. An experiment is described in which flower initiation was caused by repeated defoliation and decapitation of shoots. The control of flowering in kikuyu grass is compared with that in other plants in which removal of apical dominance allows the initiation of flower primordia on lateral branches. The importance of the utilization of the genetic potential of both hermaphrodite and male-sterile strains in any kikuyu grass breeding programme is stressed.

I. Introduction

Kikuyu grass (*Pennisetum clandestinum* Hochst. ex Chiov.), a rhizomatous, stoloniferous perennial native to East Africa from Eritrea to Uganda, is a valuable pasture grass in tropical Africa and in Australia. It was first introduced into Australia as seed from the Belgian Congo in 1919 (Whittet 1934) but there have been several subsequent introductions as cuttings from various districts in Kenya, as well as a further introduction as seed from the United States (Parker 1941). It is generally propagated by cuttings, which root freely and grow vigorously. A characteristic feature is the production of long stolons which remain unbranched or have few branches so long as they are not decapitated (Plate 1, Fig. 1). Lateral branches from the stolons may form secondary stolons or, under certain circumstances, may give rise to short erect culms bearing reduced, terminal spikes. Each spike consists of from two to five spikelets, the terminal spikelet being shortly stalked, the others sessile. The inflorescences and spikelets have been described by Stapf (1921) and by Robyns (1934). As the whole inflorescence is sessile or subsessile it is concealed within the leaf sheath of the terminal leaf of the culm (Plate 1, Fig. 2), and the only parts of the flowers normally visible are the long plumose stigmas and the anthers, which are exserted from within the leaf sheath. Each flower bears a single stigma which is bifid at the tip.

Edwards (1937) has described three strains from separate localities in Kenya. The Rongai strain is a much coarser plant than the other two, having broad, coarse leaves and thick stolons which develop rapidly after cutting. The Molo strain has narrow leaves and stolons and tends to throw up shoots from the crown after cutting. The Kabete strain is

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intermediate in leaf and stolon width and behaviour after cutting. In the Rongai strain Edwards never found exserted anthers and Parker (1941) showed that the anthers of this strain are abortive and produce no pollen. Stapf describes the upper floret as "bisexual and markedly protogynous or functionally female with rudimentary stamens", and states that the plant is functionally female in the Transvaal. Plants collected at Ankober, Abyssinia, were also functionally female, but in the anthers of these plants, in addition to "pollen mother cells which had not got beyond the stage of division", some empty pollen grains were found (Stapf 1921). Hrishi (1952) observed normal meiosis in material cultivated at the Millet Breeding Station, Coimbatore, India, but found that all the pollen mother cells degenerated after tetrad formation. Abnormal growth of tapetal tissue was held responsible for the degeneration of the pollen mother cells. At Coimbatore reproduction in *P. clandestinum* was therefore entirely vegetative and no seeds were found. In South Australia seed has been found only on the Kabete strain. Seeds and seedlings have been observed in other areas of Australia (Whittet 1934; Cross 1936, 1937; Cullity 1948; Anon. 1954) but no information is available by which the seed setting in these cases might be referred to Edwards's strains. Edwards (1937) found a few seeds on plants of the Rongai strain and suggested that "it is most probable that these seeds have been produced by cross pollination from nearby plots of the other strains". It seems clear that some strains of kikuyu grass are functionally female while others, such as Kabete, which form seeds are hermaphrodite. Since male-sterility has been observed under a wide variety of climates one may conclude that it is genetically determined, and that male-sterility is inherited.

II. Influence of Cutting and Grazing on Flowering

Edwards (1937) observed flowering on kikuyu grass only in short herbage and carried out experiments in which exsertion of stigmas and anthers was noticed in swards kept short by monthly cuts. Parker (1941) found that flowering occurred in South Australia also in swards kept short by cutting. Flowering undoubtedly occurs widely under grazing conditions, although the flowers are so inconspicuous that they have probably been overlooked. There are no records of flowering in Victoria, although flowering has been reported from Queensland, South Australia, and Western Australia. In the summer of 1954-55 close examination of grazed or mown plants around Melbourne always revealed the presence of exserted stigmas, although in long, uncut or ungrazed herbage flowering was rarely seen. However, it is not clear, either from Edwards's experiments or from these field observations, whether grazing and mowing causes the *initiation* of flowers on plants which would otherwise remain quite vegetative or whether it merely stimulates flower primordia already present to develop further. A small experiment was therefore carried out to ascertain the effect of severity of defoliation on the initiation of flowers.

III. Experimental

On February 4, 1955, 50 cuttings of non-flowering stolons were taken from plants growing in the garden at the Botany School, University of Melbourne. The cuttings, 5-6 in. long, were planted in soil in 5-in. pots, one to each pot, and kept in a greenhouse used for photoperiodic experiments (supplementary illumination between 11 p.m. and 2 a.m., about 100 ft. candles at plant height). Towards the end of February the plants had developed considerably, some having stolons more than a foot long. Sample shoots were taken from a number of the plants and examined for the presence of flower primordia. All the shoots examined proved to be strictly vegetative. The suppressed lateral buds on the stolons were found to have initiated up to five leaf primordia. The axillary bud of a node subtending an internode of just over 1 cm in length had four leaf primordia.

On February 22, 20 plants were severely defoliated. The shoots were cut back to a length of 3-4 in. and the laminae of the leaves cut back to within about a quarter of an inch of the leaf sheaths. The remaining 30 plants were not defoliated and were kept as controls. After a week 10 of the defoliated plants were again trimmed so as to remove all green tissue and growing tips. These plants were trimmed again a week later. The remaining 10 plants were not defoliated subsequent to the first treatment.

On April 15, stigmas were exserted on one of the repeatedly defoliated plants and from then on flowers have continued to appear up to the present date (July 1955). As growth was resumed by the production of unbranched stolons from the crown, flowering became more and more sparse. (Small cuttings of the Kabete and Rongai strains received from the Waite Institute, Adelaide, also flowered but ceased to do so as rapidly growing stolons appeared.) Anthers were never exserted from the experimentally induced flowers and on examination proved to be empty and functionless. In this respect and in their coarseness the plants used resemble the Rongai strain.

At the end of May the plants were moved to an unheated greenhouse under natural day lengths. Flowers continued to be produced on the 10 plants which had already produced flowers. The control (not defoliated) and the once defoliated plants have not produced flowers and no microscopic flower primordia have been found on them.

IV. Discussion

It is evident that apparently vegetative plants of kikuyu grass are in a state of "ripeness to flower", but that flowers are not formed until the plants are severely defoliated and the dominating influence of the growing point of the stolon is removed by decapitation. Flowers are then formed on short lateral shoots of the stolons from axillary buds which are normally suppressed. Each short lateral bears at least five leaves

preceding the terminal inflorescence. This means that the lateral apices probably begin to form spikelets immediately the dominating influence of the stolon tip, and possibly also of the leaves, is removed. Flowering is localized to stolons which have been defoliated and decapitated (Plate 2). It is of interest that Gardner and Loomis (1953) have found that in *Dactylis glomerata* L. a state of "ripeness to flower" may be induced by low temperatures and short days, but that the actual initiation and subsequent development of flowers require long days. Nothing is yet known of the interaction of day length and temperature in the flowering response of kikuyu grass to cutting. Wareing (1953) caused the precocious initiation of male cones in *Pinus sylvestris* by injuring the terminal winter buds of the branches. Reece, Furr, and Cooper (1949) have shown that the lateral buds of the Haden mango (*Mangifera indica* L.), which normally do not develop or remain vegetative, can be induced to form flowers if the terminal buds of the branches are removed. These experiments show that in some plants reproductive organs may not form in the presence of a dominant shoot apex and that the removal of the dominance enables flowers to be initiated on the lateral shoots. There is considerable evidence (see Lang 1952) that auxin may play a part in the suppression or initiation of flower primordia, and the dominance of leader shoots is ascribed to the flow of auxin from them. If that is so, then decapitation and severe defoliation of kikuyu grass shoots may enable flowers to form because of a reduction in the amount of free auxin in the shoots. It should be possible to imitate this situation by spraying the plant with auxin antagonists, and experiments of this nature are contemplated.

In view of the economic importance of kikuyu grass it is surprising that no work has been undertaken to select strains for different localities or to improve existing strains. It is clear that there is abundant variation even within the limited range of material introduced to Australia. Even within seedlings from the Kabete strain alone, Parker (1941) was able to distinguish seven different growth forms. If, as suggested by Parker, such a selection programme were limited to the seed-producing strain, Kabete, then a considerable reserve of variation in the other strains would remain untapped. If, however, the Rongai strain, and possibly other non-seed producing strains such as that which is common in Victoria, are female, then it should be possible to cross these with pollen from the Kabete strain. There is some evidence that the male-sterile strains are more vigorous than the hermaphrodite. In Kenya, Edwards (1937) found that the Rongai and Molo strains gave heavier yields in a treatment of close cutting than the Kabete, but the Molo strain was less capable of withstanding frequent defoliation under dry conditions. It is of interest that the early introductions of the Molo strain into South Australia did not succeed (Parker 1941). It is possible that the widespread distribution of the male-sterile strains may be an accident of introduction, both in

Africa and in Australia, but it is equally possible that they are inherently more vigorous than the fertile strains.

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Addendum

Since this paper was prepared for the press a publication dealing with the cytology of two strains which resemble the Rongai and Kabete strains of kikuyu grass has appeared (Narayan 1955). Both strains were found to have the same chromosome number, $2n = 36$. (Hrishi (1952) also found $2n = 36$, and preliminary counts on the Melbourne material give the same number.) Meiosis in the Kabete-like strain was normal and 80 per cent. of the pollen viable (stainable). Three causes of pollen degeneration, spindle and cytokinesis abnormalities and tetrad irregularities, contribute to the malformation of the pollen in the other strain, but the tapetum is said to be normal (cf. Hrishi 1952). In the majority of embryo sacs of both strains aposporic (diploid) and normal embryo sacs are formed, polyembryony being common. The Rongai-like strain produced seed when pollinated from the Kabete-like strain. From the 20 seeds (100 pollinations) seven plants were raised, two of which resembled the female parent and the other five the male parent. We cannot agree, however, with Narayan's view that the reproduction by seed of the maternal type is due to the stimulation of development of diploid, aposporic

egg cells by pollination without fertilization. If this were true then such aposporic egg cells should *occasionally* give rise to embryos without pollination, but such embryos or seeds have not been described for Rongai-like strains. There is, in fact, no evidence of apomixis in *P. clandestinum* other than Narayan's observations of diploid embryo sacs, which may or may not be viable. We would suggest that it is more likely that one of the parents is heterozygous for male-sterility, which may be dominant or recessive to the normal condition. In the experiment reported the number of progeny raised is too small for any genetical conclusion to be drawn. Narayan's work clearly supports the views put forward by us, and in particular confirms the suggestion that certain strains of kikuyu grass are genetically male-sterile. From the point of view of developmental genetics, the influence of genetic factors in disturbing meiosis in the formation of pollen but not in the formation of embryo sacs offers an attractive problem for further experiments.

FLOWER INITIATION IN KIKUYU GRASS

Fig. 1.—Vegetative plant of kikuyu grass showing the long unbranched stolons. This was one of the control plants used in the experiment reported in the text.

Fig. 2.—Close-up of culm showing exserted stigmas.

FLOWER INITIATION IN KIKUYU GRASS

Plant showing flowers (marked with arrows) induced experimentally. Photographed at end of May 1955. Note the absence of culms on the secondary stolon near the ruler, and vegetative shoots arising from the crown.

AIR-TIGHT STORAGE OF GRAIN; ITS EFFECTS ON INSECT PESTS

II. *CALANDRA ORYZAE* (SMALL STRAIN)

By S. W. Bailey*

(*Manuscript received September* 23, 1955)

Summary

The independent and joint effects of lowered oxygen tensions and increased carbon dioxide tensions on the adult and immature stages of *Calandra oryzae* L. (small strain) have been examined. The concentrations of the two gases that occurred among infested grain stored in air-tight containers have been measured. It is concluded that the death of the insects was due to the depletion of oxygen and that the associated accumulation of carbon dioxide played only a minor role.

The young immature stages were the most susceptible to the changing concentrations of oxygen and carbon dioxide.

I. Introduction

In paper I of this series (Bailey 1955) the effects of oxygen depletion and carbon dioxide accumulation on the adult and immature stages of *Calandra granaria* L. were described. It was shown that, when infested wheat was stored in air-tight containers, the respiration of the insects brought about a reduction in the oxygen tension in the intergranular air and that this killed the insects. The associated increase in the concentration of carbon dioxide was shown to be unimportant.

This paper describes similar experiments carried out with the rice weevil, *Calandra oryzae* L. It has been shown by Birch (1944, 1954) and Richards (1944) that *C. oryzae* embraces two strains or sibling species. Both authors report some physiological differences between the two strains, and Segrove (1951) reports a difference in the oviposition behaviour. Of particular interest is Richards's observation that the larvae of the two strains respond very differently to accumulations of carbon dioxide, the large strain ejecting far greater quantities of the frass that normally remains within the individual grains in which the larvae are developing. In view of these findings it seemed advisable to examine the responses of the two strains separately, and this paper describes work carried out on the small strain only.

II. Methods

In the majority of experiments the insects were exposed to constant streams of the desired gas mixtures in order to sweep away all respiratory products. Control insects were exposed to a stream of air. A general description of the apparatus employed is given in paper I (Bailey 1955).

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The origin and preparation of the insect material and of the wheat was similar to that described in the previous study except that a temperature of 29°C was employed. All experiments, and the subsequent incubation of the insects in room air, were carried out at 29°C and approximately 72 per cent. R.H., close to the optimum conditions for this species (Birch 1945).

In the present work the gradient in gas concentrations along the length of the exposure chambers was minimized by separating the experiments on the adult insects from those on the immature stages. Thus with the adult insects it was only necessary to provide sufficient grain for food, and the presence of large numbers of actively respiring immature stages was avoided. In addition, once the necessary duration of the experiments had been determined on the basis of Figure 1, it was possible to restrict the number of replicates to four per exposure chamber, each replicate containing ten 0-7 day old adults of undetermined sex. These alterations in technique reduced the absolute error in gas concentrations to ± 0.2 per cent. in the experiments on adult insects.

All adult insects were examined immediately after removal from the gas mixtures and again after 24 and 48 hr of incubation. Those showing any movement at all were recorded as alive and all results are based on the 48-hr examination.

The material used for the experiments on the immature stages was prepared as in paper I but the number of grains in each replicate was reduced to 150. Two replicates of each of the four age groups were placed in each exposure chamber. Two series of experiments were carried out, one for 7 days and one for 14 days. After removal, the grain was incubated in room air and the number of emerging insects counted. Owing to the greater number of respiring insects present in the experiments on immature stages the absolute error in gas concentrations was ± 0.5 per cent. All gas concentrations are expressed as percentages of dry gas.

III. Results

(*a*) *Effects on Adult Insects*

In view of the findings with *C. granaria*, preliminary experiments were carried out in which adult insects were exposed to concentrations of carbon dioxide in excess of those they would experience in hermetically stored grain. They survived such concentrations for longer than 4 weeks, the approximate duration of a complete life cycle at the experimental conditions of temperature and humidity. It appeared, therefore, that the response to oxygen depletion was the important factor and the choice of a suitable duration for the experiments was based on the insects' response to lowered oxygen tension.

Apart from the response to 4 per cent. oxygen, which as will be shown was a critical value, the full effects were produced within 14 days

(Fig. 1). This period was therefore chosen for all subsequent experiments on adult insects. Three series of experiments were run to determine:

(i) The effects of decreasing oxygen concentrations, carbon dioxide being absent.

(ii) The effects of increasing concentrations of carbon dioxide, oxygen being maintained at 21 per cent.

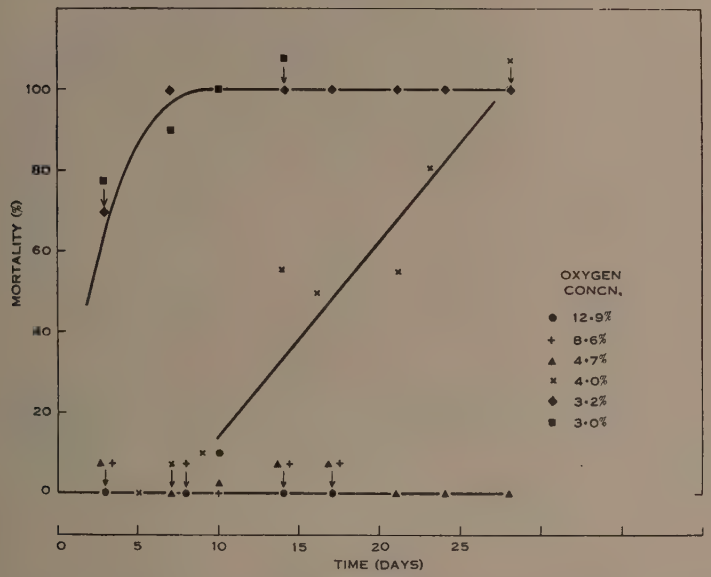

Fig. 1.—Effect of time on the mortality of adult *C. oryzae* (small strain) exposed to different concentrations of oxygen. Carbon dioxide concentration as in air.

Both responses were sharp (Figs. 2 and 3) and took place only after very considerable variations from normal atmospheric conditions occurred.

(iii) The effects of combinations of decreased oxygen and increased carbon dioxide.

When oxygen was maintained a little above a lethal minimum and carbon dioxide varied (Table 1), mortality occurred at concentrations of carbon dioxide below those found to cause death when oxygen was normal. Thus as little as 13.2 per cent. CO_2 caused complete mortality. With the opposite conditions (Table 2) complete mortality occurred when oxygen was reduced to approximately 7 per cent. The significance of these effects is related to the respiratory quotient of the insects and is discussed later.

(*b*) *Effects on Immature Stages*

Table 3 shows the separate effects of decreased oxygen and increased carbon dioxide tensions on known age groups of immature stages for 7-

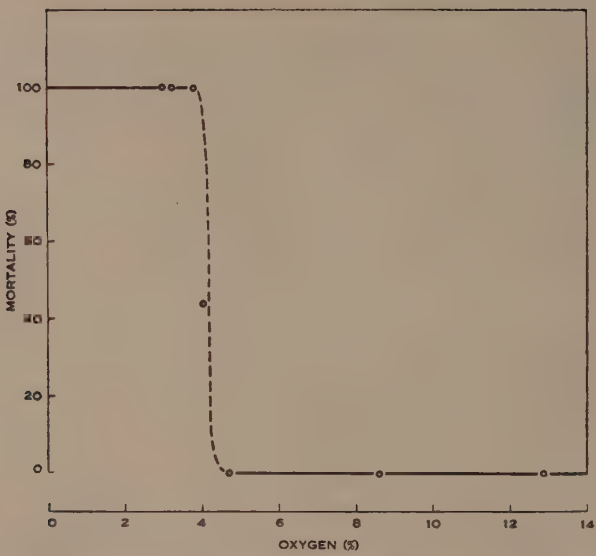

Fig. 2.—Mortality of adult *C. oryzae* (small strain) due to exposure to reduced oxygen concentrations for 14 days. Carbon dioxide concentration as in air.

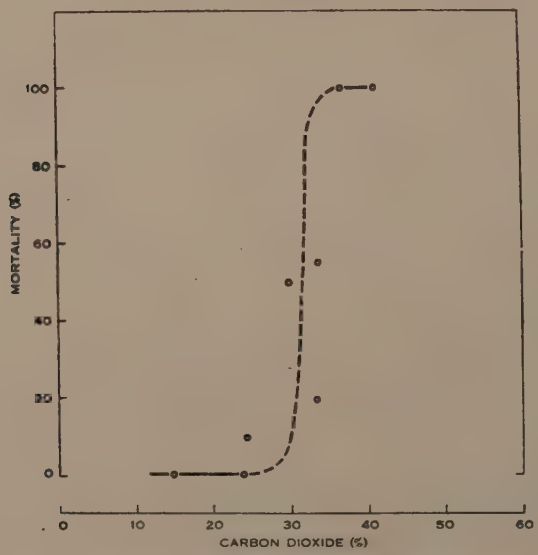

Fig. 3.—Mortality of adult *C. oryzae* (small strain) due to exposure to increased concentrations of carbon dioxide for 14 days. Oxygen concentration as in air.

and 14-day exposure periods. Controls were exposed to streams of air and showed normal emergence.

In their reaction to reduced oxygen for 7 days the 0-7 day old group showed a very marked response. The replicates exposed for 14 days showed an effect for all age groups.

TABLE 1

MORTALITY OF ADULT *C. ORYZAE* (SMALL STRAIN) DUE TO INCREASING CONCENTRATIONS OF CARBON DIOXIDE WITH OXYGEN HELD A LITTLE ABOVE A LETHAL DILUTION

Exposure period, 14 days

Carbon Dioxide (%)	Oxygen (%)	Mortality (%)
0	5.0	0
11.5	5.5	0
13.2	5.0	100
25.8	5.1	100
30.6	5.3	100

Increased concentrations of carbon dioxide for 7 days also affected the 0-7 day old group most, and exposure for 14 days caused mortality in three of the age groups. The 7-14 day old group was remarkable for its resistance to the carbon dioxide concentrations applied.

TABLE 2

MORTALITY OF ADULT *C. ORYZAE* (SMALL STRAIN) DUE TO DECREASING CONCENTRATIONS OF OXYGEN WITH CARBON DIOXIDE HELD A LITTLE BELOW A LETHAL CONCENTRATION

Exposure period, 14 days

Oxygen (%)	Carbon Dioxide (%)	Mortality (%)
20.9	25.0	0
15.6	25.5	0
11.6	27.6	10
6.8	26.9	100
5.1	25.8	100

In some cases the 21-28 day old group showed some mortality of insects which had emerged towards the end of the exposure period, indicating ability of the pupae to withstand conditions that were lethal to the newly emerged adults. With the exception of two individuals, all the surviving adults emerged during the subsequent incubation of the grain and would have been pupae during the exposure period.

Of particular interest is the finding that the immature stages, except the 0-7 day olds, had the same order of resistance as the adults to unfavourable oxygen and carbon dioxide tensions.

TABLE 3

EFFECTS OF REDUCED OXYGEN AND INCREASED CARBON DIOXIDE TENSIONS ON IMMATURE STAGES OF *C. ORYZAE* OF KNOWN AGE

The numbers in the body of the table represent the number of insects emerged as percentages of 150 (the number of grains used). Values in brackets represent proportions of total which died after emergence

Atmosphere	Emergence After 7 Days' Exposure				Emergence After 14 Days' Exposure			
Group:*	0-7 Days	7-14 Days	14-21 Days	21-28 Days	0-7 Days	7-14 Days	14-21 Days	21-28 Days
Oxygen† (%)								
15.9	44	55	54	59	49	50	49	55
9.7	30	48	42	57	31	46	57	60
7.0	28	47	47	43	19	45	51	52
5.5	5	23	16	37(8)	0	9	26	26
4.0	1	20	22	29(5)	0	7	13	21(14)
3.3	0	25	35	27(13)	0	3	10	13(12)
Carbon Dioxide‡ (%)								
10.9	40	35	44	49	37	39	38	57
17.5	32	53	60	44	51	66	58	54
20.4	36	35	43	31	37	25	36	39
24.3	27	59	34	44(1)	29	52	29	47
28.2	21	47	33	27(3)	25	50	15	31
31.1	18	54	27	19(6)	21	43	5	23(5)
35.8	7	57	23	15	5	47	2	10(5)

* Age group at start of experiment.
† Carbon dioxide concentration as in air.
‡ Oxygen concentration as in air.

(*c*) *Respiratory Quotient of the Small Strain of* C. oryzae

The respiratory quotient (R.Q.) was determined by the analysis of samples of intergranular air withdrawn from flasks completely filled with grain containing insects of known age. In all cases sufficient insects were present to swamp any effects due to the respiration of the grain.

Preliminary experiments were carried out to ascertain if any effects were due to the reduction in atmospheric pressure caused by successive sampling from the same flasks. Some apparent acceleration in the respiration rate was expected owing to the progressive reduction of the amount of air left in the flask. No other effects could be detected.

The results, shown in Tables 4 and 5, indicated for most age groups a high initial R.Q. which dropped as the concentrations of oxygen and carbon dioxide became further removed from those in normal air. In the two oldest age groups of the immature stages respiration was more rapid, and a depression of the R.Q. had probably already occurred by the time the first samples were drawn.

TABLE 4

RESPIRATORY QUOTIENT OF 0-7 DAY OLD ADULT *C. ORYZAE* (SMALL STRAIN) AT 29°C AND 70 PER CENT. R.H.

Replicate No.	Sampling Time (hr after sealing)	Carbon Dioxide (%)	Oxygen (%)	Respiratory Quotient
1	23.25	3.52	17.15	0.94
2	22.5	3.53	17.10	0.93
3	22.0	3.66	16.90	0.92
1	41.5	6.47	13.20	0.84
2	42.5	6.68	12.75	0.82
3	43.25	7.50	12.10	0.85
1				
2	68.25	11.72	6.58	0.82
3	67.5	11.35	6.90	0.83
1	91.0	14.15	2.76	0.78
2	93.25	14.55	2.55	0.79
3	94.0	15.00	1.91	0.79
1	115.5	15.20	1.45	0.78
2	115.0	14.73	1.48	0.76
3	114.5	15.40	1.43	0.79
1	163.0	15.84	0.63	0.78
2	163.5	15.75	0.74	0.78
3	165.5	15.95	0.57	0.79

This high R.Q. at the start of the experiments was even more marked in some check experiments on immature stages which are not included in the tables. In these the number of insects present and, therefore, the total respiration rate were kept very low. The R.Q.'s were above unity until oxygen had dropped to approximately 18 per cent. After this, the R.Q.'s dropped in conformity with the examples shown in Table 5.

IV. DISCUSSION

In a bulk of infested grain all stages of the insect will be present and the contribution made by each age group to the R.Q. of the whole population will depend on its relative abundance and its respiratory rate. The numbers of a stage present will tend to be in proportion to the duration of that stage. Thus adults with a life of some months will predominate but the 14-21 day old group of immature stages will have

TABLE 5

RESPIRATORY QUOTIENT OF FOUR AGE GROUPS OF IMMATURE *C. ORYZAE* (SMALL STRAIN) AT 29°C AND 70 PER CENT. R.H.

0-7 Days Old			7-14 Days Old			14-21 Days Old			21-28 Days Old		
Repl. No.	Hr After Sealing	R.Q.	Repl. No.	Hr After Sealing	R.Q.	Repl. No.	Hr After Sealing	R.Q.	Repl. No.	Hr After Sealing	R.Q.
1	21.0	0.90	1	25.25	0.92	1	21.75	0.85	1	22.0	0.74
2	21.5	1.03	2	16.5	0.91	2	18.75	0.87	2	26.0	0.73
						3	17.5	0.82			
1	51.0	0.84	1	47.5	0.86	1	45.5	0.83	1	48.0	0.71
2	46.5	0.88	2	43.25	0.82	2	47.0	0.81	2	50.0	0.70
						3	46.0	0.77			
1	72.0	0.83	1	74.0	0.82	1	66.75	0.83			
2	70.25	0.83	2	64.75	0.79	2	67.0	0.80	2	70.0	0.70
						3	67.25	0.78			
1	98.0	0.81	1	97.5	0.80	1	91.75	0.83			
2	93.5	0.81	2	89.75	0.79	2	92.75	0.80			
1	123.0	0.79	1	119.5	0.79						
2	117.5	0.81	2	115.0	0.78				2	119.25	0.71
1	151.25	0.79	1	143.25	0.80						
2	142.5	0.79				2	139.25	0.82	2	142.0	0.72
						3	143.5	0.79			
1	174.0	0.79	1	167.5	0.80	1	161.5	0.84			
2	167.0	0.79	2	167.0	0.78						
			1	191.5	0.79						
2	193.75	0.78	2	189.5	0.79						

an effect owing to its very high respiratory rate (Howe and Oxley 1944; Birch 1947). Figure 4 indicates the combinations of oxygen and carbon dioxide most likely to occur among grain infested by the species and makes allowance for the two factors above. The points fall on a slight curve.

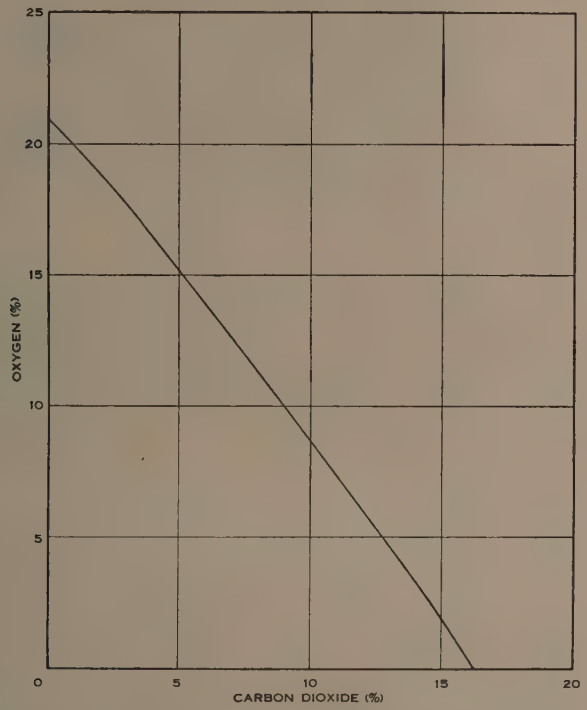

Fig. 4.—Concentrations of oxygen and carbon dioxide occurring among grain infested with *C. oryzae* (small strain).

Dendy and Elkington (1920) measured the R.Q. of adult *C. oryzae* employing the method due to Krogh. They gave a value of 0.77 at 30°C. This is low compared with the present results as the gaseous conditions in their experiments were closest to that of the first group of Table 4. In 1920, however, two strains of *C. oryzae* were not recognized and the identity of their material is not certain, although it was most probably the small strain as it was derived from wheat (Birch 1954). Birch (1947) also determined the R.Q. of the adults of the small strain using the Warburg technique. He did not measure oxygen consumption and carbon dioxide production simultaneously, an admitted defect, and gave a value of 1.10 at 30°C. His method absorbed carbon dioxide as it was produced, and the duration of the experiments were such that any effects due to

oxygen depletion would have been very slight. The trend in Table 4 suggests that under these conditions the R.Q. might well be above the values in the first group of the table. However, the R.Q. of the insects in normal oxygen tensions is of lesser interest here as the respiration of the insects rapidly alters the concentrations of oxygen and carbon dioxide.

Figures 4 and 5 show that a maximum concentration of approximately 16 per cent. of carbon dioxide was attained and that oxygen was reduced to a very low concentration, a minimum of 0.06 per cent. having been recorded. From the determinations of the independent effects of the two gases (Figs. 2 and 3) it is clear that the reduction of oxygen was responsible for the death of the insects. At a R.Q. of 0.8 the associated carbon dioxide present would have only a small effect, raising the oxygen level at which 100 per cent. adult mortality occurred from 3.8 per cent. to approximately 5 per cent.

Dendy and Elkington (1920) concluded that carbon dioxide had a poisonous effect independently of oxygen tension. In a series of four experiments they sealed weevils and grain in gas tubes containing from 14 to 78 per cent. of carbon dioxide and oxygen at approximately atmospheric concentration. After the insects had died they analysed the contents of the gas tubes. In two of these experiments the carbon dioxide was always above 50 or 78 per cent. respectively, the oxygen concentration only dropping a few per cent., and the insects quickly died as would be expected from Figure 3. In the other two experiments, however, the carbon dioxide was only 14.1 and 23.2 per cent. at the start and rose to 22.6 and 24.6 per cent. respectively at the finish. Oxygen dropped to 13.9 and 19.1 per cent. respectively. Nevertheless, the insects died. As the findings in the present work would not account for this, two check experiments were carried out using the constant gas flow method and arranging the gas mixtures to be as unfavourable during the whole exposure period as they were at the termination of Dendy and Elkington's experiments. The combination of gas used was 13.6 per cent. oxygen and 23.3 per cent. carbon dioxide. One experiment ran for 17 days, the other for 28 days, both being substantially longer than the period employed by Dendy and Elkington. In both instances no mortality at all occurred. The reason for the mortality found by the earlier investigators cannot be explained. However, they used chemically prepared nitrogen and it is possible that traces of impurities, particularly oxides of nitrogen, were present in their gas tubes.

The experiments on the immature stages (Table 3) showed that no effects were apparent until very substantial differences from normal atmospheric conditions occurred. The importance of oxygen depletion was again demonstrated, no effects being produced by carbon dioxide up to those concentrations possible on the basis of Figure 4.

Some indication of the effects of combinations of low oxygen and high carbon dioxide is shown in Figure 5. Although it is impossible to

know when death occurred it is probable that conditions became highly unfavourable where the curves tend to flatten out. The indications are that, in the two youngest age groups, death occurred at oxygen tensions that were above those causing mortality in the absence of carbon dioxide.

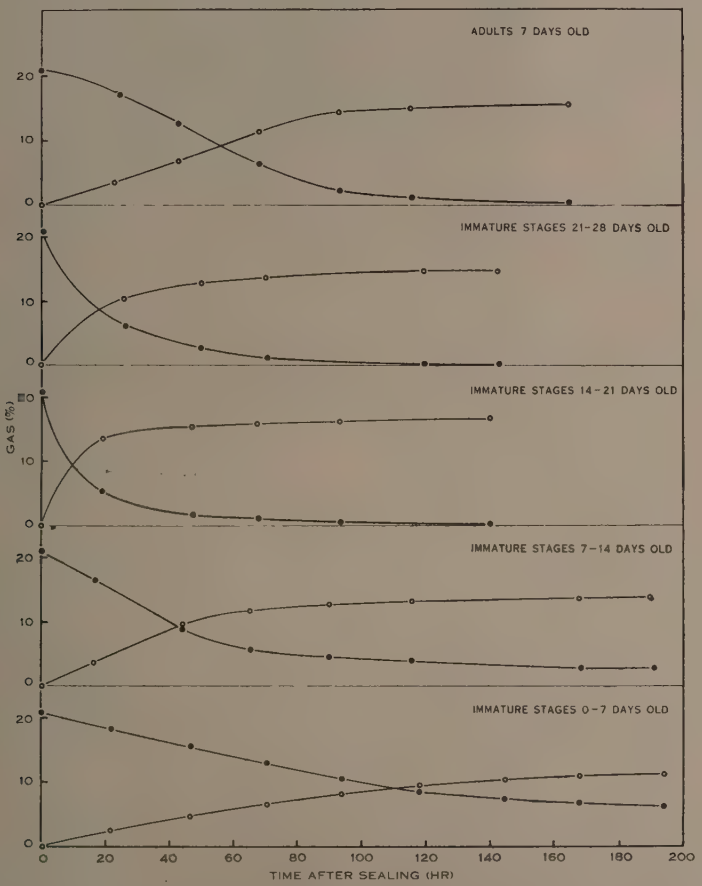
ADULTS 7 DAYS OLD
IMMATURE STAGES 21-28 DAYS OLD
IMMATURE STAGES 14-21 DAYS OLD
IMMATURE STAGES 7-14 DAYS OLD
IMMATURE STAGES 0-7 DAYS OLD
GAS (%)
20
10
0
0 20 40 60 80 100 120 140 160 180 200
TIME AFTER SEALING (HR)

Fig. 5.—Typical oxygen consumption and carbon dioxide production of various stages of *C. oryzae* (small strain) in sealed containers at 29°C and 70 per cent. R.H. ● Per cent. oxygen. ○ Per cent. carbon dioxide.

In one flask containing wheat infested with 0-7 day old immature stages, gas exchange ceased when oxygen was still above 15 per cent. and carbon dioxide was 4 per cent. Dendy and Elkington (1918) report a similar instance in which death of young immature stages occurred in a sealed flask which on analysis contained only 3.93 per cent. of carbon dioxide. There is some evidence, therefore, suggesting that a very critical

stage is passed through. Further experiments with insects of more precisely known ages are necessary. If confirmed this finding might be of considerable practical importance as it may be possible to eradicate an infestation in grain, stored for a suitable period in silos having a much lower standard of sealing than otherwise necessary.

The adults were able to reduce the oxygen tension to very low values, 0.06 per cent. in one instance. A similar finding was reported with *C. granaria* and possible mechanisms discussed (Bailey 1955). Of the immature stages the two oldest age groups showed a similar ability (Fig. 5) and these were also the groups that were most resistant to low tensions of oxygen. The two younger age groups did not reduce the oxygen so much. However, the final concentration depended, in part, on the total respiration rate within the flask; where this was high, oxygen was reduced to lower concentrations. The relatively lower respiration rate of the two younger age groups made it impossible to expose them to the rapid drop in oxygen tension experienced by the older larvae and pupae. This could not be compensated for by extending the time factor as the aging of the insects caused the age grouping to alter.

It will be seen from Figure 5 that the respiratory rates of the various age groups agree approximately with the trend shown by Howe and Oxley (1944) and by Birch (1947). Close agreement was not to be expected as the number of insects in each age group was not identical.

The period required for the elimination of live insects from a bulk of grain can be estimated by extrapolating from Table 4. At 29°C lightly infested grain producing 0.5 per cent. of carbon dioxide in 24 hr will take 25 days before conditions become lethal. If to this is added 14 days (Fig. 1) a total of 39 days is indicated. Heavily infested grain with a carbon dioxide value of 5 per cent. would require a total of 17 days. Both these totals are maximum values, as in practice the 14-day component would be shorter owing to the continued drop in oxygen tension.

V. Acknowledgments

The author wishes to express his thanks to Mr. J. B. McCabe for assistance in this work and to Mr. L. A. Marshall, who drew the figures.

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SEASONAL CHANGES IN SOIL SALINITY AT TINTINARA, SOUTH AUSTRALIA

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Summary

Measurements have been made of seasonal changes in soil salinity and soil water at Tintinara in the Coonalpyn Downs of South Australia. Five separate sites representing different soil profiles were selected for study. All soils contained saline water-tables and four of the five had varying depths of sand over finer-textured subsoils; the fifth soil was fine-textured throughout. The investigations were conducted over a 12-month period, salinity and water determinations being made every 8 weeks.

Data on soil salinity are presented as:

(1) Conductance of soil pastes, determined on replicates and statistically analysed.

(2) Percentage of total soluble salts, derived from conductivities of 1 : 5 soil-water suspensions determined on composite samples.

(3) Percentage of chlorides expressed as NaCl, determined on composite samples.

All sets of data show that soluble salts moved upwards through the soil profile during spring and summer and down during the rainy season. Where the summer water-table was within 4 ft of the surface large amounts of saline material accumulated in the top inch of soil; in one case there was an increase of from 0.019 per cent. NaCl in winter to 3.2 per cent. in summer.

Data are also presented showing that the salinity of the ground-waters increased to a maximum of 2-3.5 per cent. total salts in spring or summer. Seasonal soil water changes are recorded and discussed in relation to salinity changes.

The climatic, soil, and ground-water factors influencing salt movements are discussed and the agronomic implications of seasonal salinity changes are stressed. Suggestions on the basis of the results obtained are made respecting the sampling of saline soils.

I. INTRODUCTION

The question of the magnitude of seasonal variations in soil salinity arose during soil survey operations in the Coonalpyn Downs of South Australia. Shallow saline ground-waters were found to have widespread occurrence in association with a variety of soil profiles. Observations of these soils at different times of the year suggested that there was a significant seasonal variation in salt content. Such variations have been established in other parts of the world and it is known that the salt concentrations vary according to downward and upward flow of water in soils. Such a variation must affect the value to be placed on determinations of the salt content of soils, derived from single samples collected at any one time of the year.

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The investigation reported here was designed to estimate the magnitude of seasonal variations of salt concentration in commonly occurring but different soil profiles associated with shallow ground-water. It was expected that the results would have agronomic significance, in relation to the salt tolerance of various cultivated plants and the ability of some annual plants to complete their life cycle when the salt content of the root zone is low.

Australian research on soil salinity problems has been concerned particularly with the irrigation of incipiently saline terrain, which is very extensive in Australia. Other work has concerned the movement of salts in land to be used for arable farming. The present investigation arose in connexion with the possible use of saline soils for pasture production under natural rainfall conditions.

Numerous investigations, both overseas and in Australia, have recorded salt movements in soils. Many of the soils examined, however, were not affected by shallow ground-water (Teakle and Burvill 1938; Raupach 1951), or had a shallow water level maintained artificially in isolated soil columns (Thomas 1939; Mallik 1942). Other investigations have been concerned with yearly rather than seasonal movements of salts (West and Howard 1953). For clay soils with saline ground-water in the Jordan Valley, Ravikovitch and Bidner-Bar Hava (1948) found that for the upper 15 cm layer of soil, the percentage of total soluble salts rose from 0.17 in December to a maximum of 0.61 in February. The ground-water varied in total salt content from 3.72 to 5.1 per cent., being slightly more concentrated in summer than in winter. Evans (1952) in New Zealand showed high salt concentrations at two depths, 0-4 in. and 4-8 in., at several sites in the summer and lower values in the late autumn and winter.

Results of other investigations in either the field or the laboratory have shown that there is appreciable variation in salt accumulation over months or years depending on the depth to ground-water, the texture of the soil, and the occurrence of downward flow of water due to rainfall. The fluctuating salt concentrations depend on water movements in the soils. The presence of ground-water in the soil provides for movement of water in the liquid phase towards the surface in dry periods, and loss of moisture to the atmosphere. Hence the accumulation of salts near the surface should depend on the magnitude of capillary movement and the concentration of salts in the ground-water balanced against the downward leaching effects of rainfall. The seasonal movement of salts in a soil affected by shallow saline ground-water shows two marked features: a dominantly upward flow of water and dissolved salts in dry periods, and their dominant downward flow in wet periods. The ultimate predominance of one or the other trend depends on a number of factors: the physical properties of the soil, its exposure to atmospheric effects, the depth to ground-water, the concentration and nature of dissolved substances, the

amount and distribution of rainfall, the air temperature, and the quantities of ground-water available for evaporation.

Many of these factors have had little attention so far. Generally it appears that upward flow of moisture may be appreciable from ground-waters from 3 to 6 ft below the surface, but it has been claimed that moisture ascends to the surface from ground-water levels at 22 ft (Vaidhianathan and Luthra 1935). The physical properties of soils in relation to water movement have been studied principally on soils either mainly clay or mainly sand; but no work is reported on soil profiles, common in the Coonalpyn Downs, involving a variable depth of sand over a clayey subsoil.

II. General Description of the Area

The Coonalpyn Downs is the name given to an area of several thousand square miles formerly known as the Ninety-mile Desert or Plain in the south-east of South Australia and extending from the coast to the Victorian border. Essentially it is a sandy plain broken in its western part by a series of limestone ranges, trending north-west to south-east, and rising 100-200 ft above the plain. The secondary features are a large number of east-west sand ridges, undoubtedly of aeolian origin. The plain rises at the east to an elevation of about R.L. 400 ft at the interstate boundary and there is also a slight rise to the south. At Tintinara, the railway station nearest to the sampling sites, the elevation is R.L. 62 ft.

Surface drainage is almost indiscernible, owing to the low flat terrain and the porous nature of the country. In some places, however, there is a sluggish northerly movement of surface water, and any tendency to flow westward is checked by the limestone ranges. Water therefore is confined to the corridors and plains between these ranges. Large expanses are subject to inundation in wet seasons, and even larger areas have ground-water a few feet below the surface. This ground-water varies in salt concentration and depth, being deeper and less saline to the east and shallower* and more saline to the west. In the Tintinara district and many places south and west, there is saline ground-water, and in low-lying areas this rises in winter to give shallow salt lakes. Water is held also in deeper aquifers throughout the Coonalpyn Downs, and these are normally a source of subartesian water of lower salinity. At Tintinara, however, the water from aquifers 200-300 ft deep is artesian.

The natural vegetation of the Coonalpyn Downs generally consists of a moderately dense cover of various shrubs, often referred to as heath, with frequent mallee and occasional eucalypt trees. Saline sites are usually marked by sparser vegetation and distinctive species such as samphire (*Salicornia* (?) sp.), thatching grass (*Cladium filum* (Labill.) R.Br.),

* The terms deeper and shallower refer only to the distance from the surface to the water-table.

Australian salt grass (*Distichlis distichophylla* (Labill.) Fassett), low broombush (*Melaleuca oraria* J. M. Black), and salt water tea-tree (*Melaleuca halmaturorum* F. Muell.).

The soils generally have sandy surfaces and fine-textured subsoils at varying depths and with columnar structural features. High contents of soluble salts are common in the soils, especially in the subsoils, particularly where saline ground-water occurs close to the surface. The nature and distribution of the soils in the Tintinara district have been reported by Jackson and Litchfield (1954). Other portions of the Coonalpyn Downs have been described by Taylor (1933), Coaldrake (1951), and Blackburn *et al.* (1953).

TABLE 1

MEAN RAINFALL AT TINTINARA, 1911-1940, AND MEAN TEMPERATURES AT KEITH, 1947-1953

Data	Jan.	Feb.	Mar.	Apr.	May	June	July
Rainfall (in.), Tintinara	0.64	0.88	0.78	1.30	2.11	2.26	2.04
Temperature (°F), Keith	70	67	65	58	54	51	49

Data	Aug.	Sept.	Oct.	Nov.	Dec.	Year
Rainfall (in.), Tintinara	2.25	2.21	1.60	1.22	1.09	18.38
Temperature (°F), Keith	51	54	58	61	67	59

The main feature of the climate is the alternation of hot dry summers with cool wet winters. Data on rainfall at Tintinara and air temperature at Keith, 22 miles to the south-east, are presented in Table 1.

III. Descriptions of Sampling Sites

The sampling sites were chosen to represent the extensive saline areas mapped during the soil survey of the area (Jackson and Litchfield 1954). The five sites occur in three distinct areas, two of which have been cultivated, the other being virgin land. Three of the sites, 1*A*, 1*B*, and 1*C*, occur close to each other on a sandy bank near a saline swamp. The location of the sites in the Tintinara district is shown in the locality map (Fig. 1) in relation to the saline and moderately saline areas. Saline ground-water occurs at all the sample sites within 60 in. of the surface, as well as in other salt-affected parts of the Tintinara district. The location of sites 1*A*, 1*B*, and 1*C* in relation to topography, soil profile, and ground-water is shown on the section diagram (Fig. 2). These three sites differ in the depth to ground-water and in the depth of sand over the clay subsoil, but the diagram shows that this results from variations in the depth of sand over a fairly level subsoil and ground-water. All but site 2 have a general soil profile of varying depths of loose sand over a compact

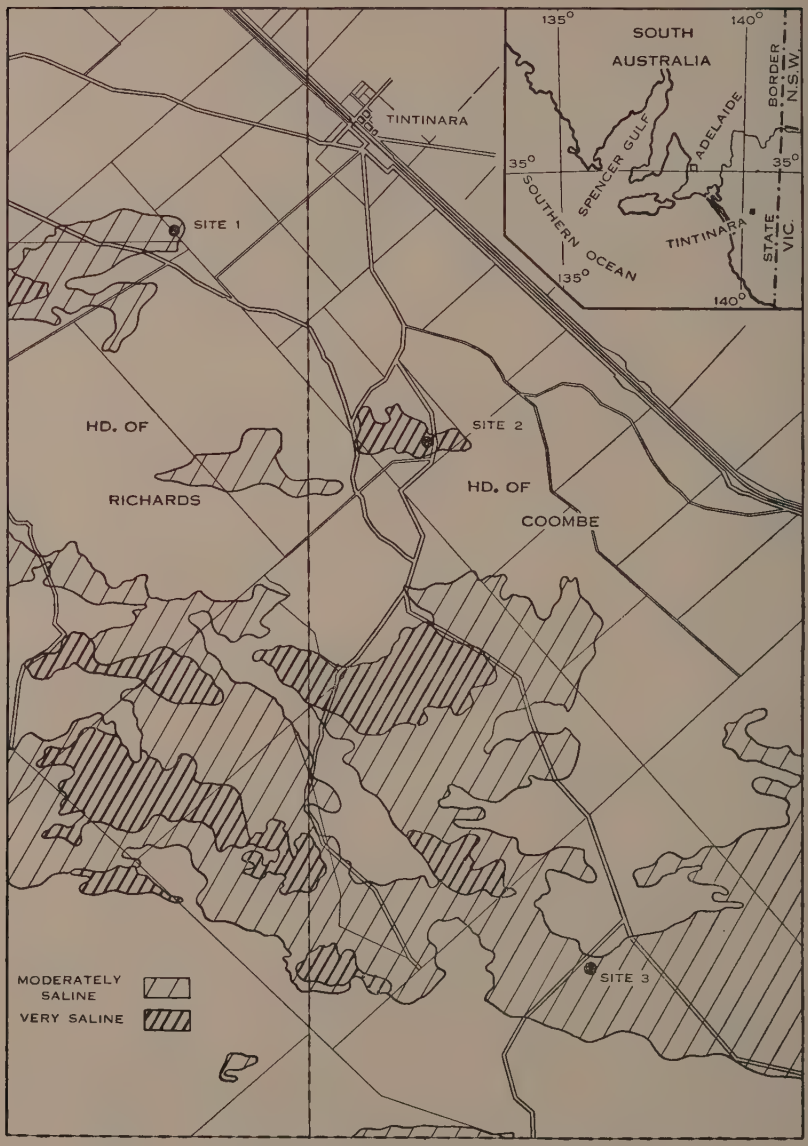

Fig. 1.—Locality map showing distribution of moderately and very saline soils in the Tintinara district, S.A.

subsoil. In site 2 the profile is mainly clay with a thin cover of sandy loam or loam. Site 2 is the only virgin one, as its greater salinity and swampy nature have prevented agricultural activities so far.

The main features of the sites are set out below.

(*a*) *Sites* 1A, 1B, *and* 1C

These are located in Section 97, Hundred of Richards, the property of Messrs. J. and E. L. Northey, and lie close together on a cultivated sand rise south-east of a saline swamp. The sites are curved areas, roughly on the contours, at different levels and distances from the swamp. This swamp has a cover of samphire and thatching grass and holds a few inches of water in winter. A thin salt crust appears on its dry surface in summer.

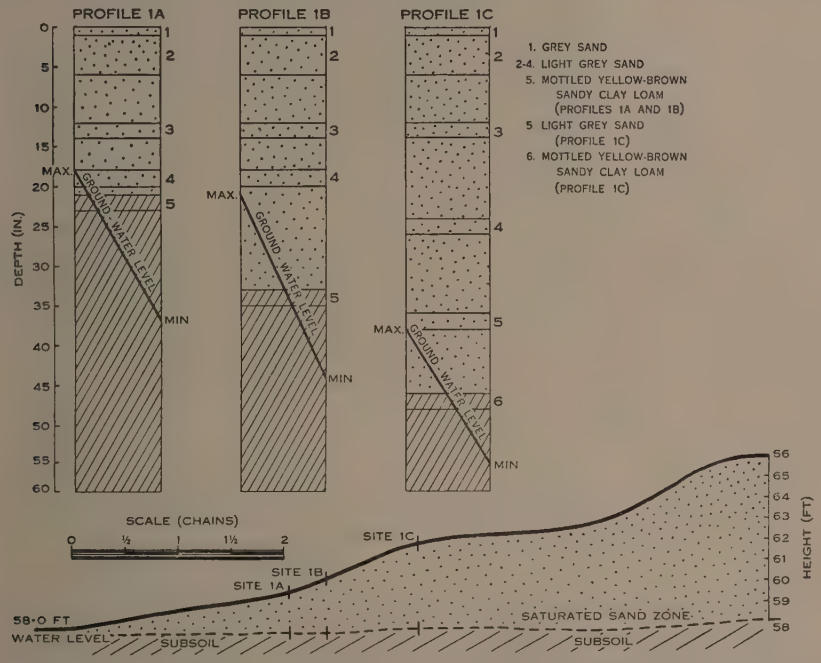

Fig. 2.—Cross section of sand dune showing position of sites 1*A*, 1*B*, and 1*C*. Profile characters, sample depths, and ground-water occurrences are also shown.

Analyses of the salt crust showed a preponderance of chloride, a small amount of sulphate, and a trace of bicarbonate. It appears that approximately three-quarters of the salt crust consisted of sodium chloride, the balance being mainly calcium sulphate (gypsum) but including small amounts of sodium sulphate and calcium bicarbonate. The natural vegetation on the sand rise used for the sites consisted mainly of shrubs and sedges at lower levels with shrubs and a few trees at higher levels. The three sites lie inside a small paddock which was cleared and sown with lucerne in 1949. The growth of this plant shows variation apparently due to salinity; the stand has been more productive on higher ground and has died out on the low fringe of the saline swamp. Other pasture species

in the paddock include strawberry clover (*Trifolium fragiferum* L.), subterranean clover (*Trifolium subterraneum* L.), and Wimmera ryegrass (*Lolium rigidum* Gaud.). Plants of limited grazing value include the annual grasses: silver grass (*Vulpia myuros* (L.) Gmel.) and barley grasses (*Hordeum* spp.), and cape-weed (*Cryptostemma calendula* (L.) Druce).

The location of the sites was influenced by pasture variation and by variations in soil profiles. The following pasture characteristics of the different sites are important.

Site 1*A* had a sparse growth of annual plants of limited grazing value, the main grasses in winter and spring being barley grass, silver grass, and bromes. Other plants recorded in November 1953 were coast barb grass (*Pholiurus incurvus* (L.) Schinz & Thell.), cape-weed, *Polypogon maritimus* Willd., and isolated plants of cereal barley, Wimmera ryegrass, and strawberry clover.

Site 1*B*, approximately 15 yards up slope from site 1*A*, had a denser and more vigorous growth of similar plants. In November 1953, plants of cereal barley, Wimmera ryegrass, and strawberry clover were more numerous than on site 1*A*, but certainly not major constituents of the pasture.

Site 1*C*, a further 15-22 yards up slope from site 1*B*, was the only sample site with a reasonable pasture growth. In November 1953 the main plants were lucerne (*Medicago sativa* L.), strawberry clover, Wimmera ryegrass, brome (*Bromus* sp.), cape-weed, subterranean clover, silver grass, haresfoot clover (*Trifolium arvense* L.), clustered clover (*T. glomeratum* L.), and shaftal clover (*T. resupinatum* L.).

The general profile characteristics of the three sites, and the depths at which samples were taken periodically, are shown in Figure 2. Laboratory examinations of composite samples from each site were made to show the qualities of the different horizons sampled. The results, in Table 2, show the mechanical composition, organic matter as indicated by nitrogen content, and pH. The significant features are: (i) a fairly uniform mechanical composition of loose sands on all three sites; (ii) absence of organic matter in the sand, except for the upper two samples; (iii) the uniform mechanical composition of subsoils; (iv) the absence of silt fractions.

In December 1953 an artesian bore was put down near site 1*C*. This bore delivers water from Oligocene deposits at 305 ft and the water rises 4 ft above the bore site with a discharge of 800 gal/hr. It was noticed at the January collection of samples that discharge of water was occurring fairly freely into the soil but the free flow continued for a few weeks only. It is possible, however, that the drainage of this water has affected the hydrology and salinity of some positions in site 1*C*.

TABLE 2

ANALYTICAL DATA FOR SOIL SAMPLES AT SITES 1*A*, 1*B*, AND 1*C*

Determinations for oven-dry soil on composite samples, July 1954

Site	Sample	Depth (in.)	Field Texture*	pH	Nitrogen (%)	Moisture (% air-dry soil)	Loss on Ignition (%)	Clay (%)	Silt (%)	Fine Sand (%)	Coarse Sand (%)
1*A*	1	0-1	S	8.6	0.050	0.6	1.6	3	1	59	37
	2	1-6	S	8.6	0.022	0.3	0.9	3	—	64	33
	3	12-14	S	9.0	n.d.	0.2	0.4	3	—	65	32
	4	18-20	S	9.0	n.d.	0.6	0.4	3	—	67	30
	5	20-22	SCL	9.5	0.013	2.8	1.3	14	—	60	26
1*B*	1	0-1	S	7.5	0.049	0.5	1.6	3	—	58	39
	2	1-6	S	7.5	0.032	0.5	1.4	3	—	63	34
	3	12-14	S	8.0	n.d.	0.2	0.3	2	—	65	33
	4	18-20	S	8.5	n.d.	0.2	0.3	2	—	67	31
	5	32-34	SCL	9.5	0.014	3.1	1.5	15	—	58	27
1*C*	1	0-1	S	7.0	0.052	0.5	1.7	2	2	59	37
	2	1-6	S	6.5	0.025	0.4	1.0	3	1	62	34
	3	12-14	S	7.5	n.d.	0.2	0.4	1	1	59	39
	4	24-26	S	8.0	n.d.	0.2	0.3	1	1	66	32
	5	36-38	S	8.6	n.d.	0.3	0.3	1	1	67	31
	6	44-46	SCL	8.6	0.011	3.5	1.5	16	—	56	28

* S, sand. SCL, sandy clay loam.

(*b*) *Site* 2

Site 2 is in Section 37/N′ of the Hundred of Coombe, the property of Mr. C. A. Zadow. The Section is made up largely of an extensive flat saline area, probably a former lagoon. The soil is mainly black clay to 12 in. over a calcareous clay or marl. Saline ground-water varies in depth from about 12 to 40 in. seasonally. The site was near the edge of the extensive saline area and levels obtained showed a relief of less than 2 in.

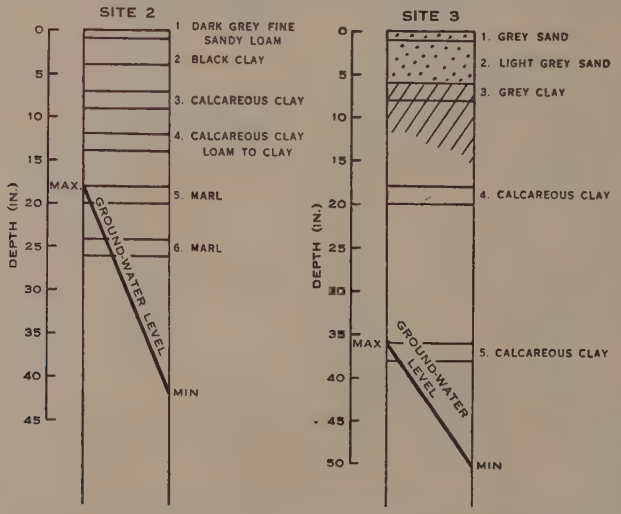

Fig. 3.—Profile features, sample depths, and ground-water levels for sites 2 and 3.

The native perennial vegetation is fairly uniform and dense considering the salinity, but does not provide a continuous ground cover. The plants are mainly thatching grass, Australian salt grass, two other grasses (*Agropyrum* sp. and *Danthonia* sp.), and isolated specimens of samphire. The fringe of the flat, several chains away, is marked by low broombush (*Melaleuca oraria*) and dryland tea-tree (*Melaleuca pubescens* Schau.). There are small bare areas between plants on the site but the vegetation is relatively profuse for such a saline area. The features of the soil profile and depth of samples are shown in Figure 3. The results of laboratory examination of composite samples for mechanical composition, organic matter, and carbonate content are given in Table 3. These indicate: (i) the high content of colloids throughout the profile; (ii) the appreciable content of organic matter, especially in the clay; (iii) the high carbonate content at shallow depth.

(*c*) *Site* 3

Site 3 is in Section L, Hundred of Coombe, the property of Mr. I. H. Heron. It lies near the fringe of a small plain bounded on north and south

TABLE 3

ANALYTICAL DATA FOR SOIL SAMPLES AT SITE 2

Determinations for oven-dry soil on composite samples, July 1954

Sample	Depth (in.)	Field Texture*	pH	Carbonates as $CaCO_3$ (%)	Nitrogen (%)	Moisture (% air-dry soil)	Loss on Ignition (%)	Clay (%)	Silt (%)	Fine Sand (%)	Coarse Sand (%)
1	0-1	FSL	8.6	n.d.	0.101	3.4	4.3	14	15	51	20
2	1-3	C	8.3	n.d.	0.152	6.2	5.6	29	3	50	18
3	7-9	C	8.3	24	0.137	13.2	15.4	28	13	29	6
4	12-14	CL	8.6	30	n.d.	9.3	15.9	24	5	35	6
5	18-20	CL	8.6	34	n.d.	5.6	18.9	10	4	35	17
6	24-26	CL	8.6	34	n.d.	9.4	19.0	13	3	33	17

* FSL, fine sandy loam. C, clay. CL, clay loam.

by sandy hills. Prior to clearing in 1950 and sowing a pasture mixture of subterranean clover and *Phalaris tuberosa* L., there was a natural vegetation consisting mainly of low broombush, thatching grass, and mallee eucalypts. The surface of the area is quite sandy but the combination of a clay subsoil and shallow ground-water ensures waterlogging in wet winter months. In the first year of pasture establishment a large area of this flat was flooded to a depth of 18 in. This flooding killed pasture species except on the higher fringes. Surface drains were made to move water towards nearby salt lakes, and have had some effect in improving drainage.

The sample site is located midway between one of the drains and the higher fringe of the flat. Isolated, unhealthy plants of *Phalaris tuberosa* and subterranean clover occur mainly at the east end of the site. In November 1953 there was a notable growth of *Spergularia marginata* (DC.) Kitt., *Polypogon*, and *Crassula*. In January 1954 there was vigorous growth of stinkwort, *Inula graveolens* (L.) Desf. Only one plant of samphire was seen near the sample site. At a distance of 2 chains, on slightly higher ground, the introduced pasture species show reasonably satisfactory growth, but the growth on the sample site is typical of the flat area.

The soil profile (Fig. 3) consists of 6-9 in. of grey sand over a grey-brown columnar clay with an accumulation of carbonate at 24 in. and carbonate hardpan at 48 in. Free water accumulates in winter in the sand immediately above the clay, depending on season. Laboratory data on the soil at site 3 are presented in Table 4.

The site is obviously not as saline as site 2, but is comparable with site 1*A*. A thin brittle salty crust is noticeable on some patches in summer months. This site is representative of many moderately saline areas with a profile that has been named the Monkoora sand (Taylor 1933).

IV. Method of Investigation

Determinations of soluble salts and moisture were made on soil samples from selected depths on each of five sites at 2-monthly intervals from July 1953 to July 1954. Each site consisted of a strip of land selected so as to have a fairly uniform soil profile. Four of the sites were linear or curved strips, 1-4 chains long and approximately $\frac{1}{4}$ chain wide. The other site, 2, was an annular strip.

At each sampling period determinations were made on samples taken from six replicate profiles on each site. The layers for sampling were chosen to represent important horizons in each soil profile; minor changes had to be made at times in all but site 2 to accommodate profile variation. Replicate sample points were distributed evenly over each site. Composite samples, representing equal parts from each replicate, were collected in air-tight containers for laboratory determinations. A determination of soil paste conductance was made in the field on each replicate sample,

TABLE 4

ANALYTICAL DATA FOR SOIL SAMPLES AT SITE 3

Determinations for oven-dry soil on composite samples, July 1954

Sample	Depth (in.)	Field Texture*	pH	Carbonates as $CaCO_3$ (%)	Nitrogen (%)	Moisture (% air-dry soil)	Loss on Ignition (%)	Clay (%)	Silt (%)	Fine Sand (%)	Coarse Sand (%)
1	0-1	S	8.4	n.d.	0.037	0.5	1.3	2	1	61	36
2	1-6	S	8.4	n.d.	0.017	0.4	0.8	2	2	63	33
3	6-8	C	8.8	n.d.	0.047	5.5	3.1	27	1	47	25
4	18-20	C	8.8	28	n.d.	7.6	15.2	17	9	31	15
5	36-38	C	8.8	14	n.d.	8.3	8.7	21	7	35	23

* S, sand. C, clay.

using a polystyrene cup (Hutton 1954) inserted in the circuit of a portable Wheatstone bridge (Aitchison 1953). Soil pastes were made up with distilled water in waxed paper cups, transferred to the polystyrene cup and adequately tamped to exclude air. The logarithm of resistance (R), given by the instrument, was converted to conductance (C) so that $C = 10^4/\text{antilog } (\log R)$. Paste temperatures were not determined, but it is estimated that the conversion of all readings to a uniform temperature basis of 60°F would vary the results by approximately 10 per cent. The conversion would reduce the conductance values in summer and increase the winter values.

The field determinations of soil paste conductance constituted the main data and were used to obtain mean values for conductance at the selected depths at different periods of the year. Mean conductance values were obtained also for ground-waters sampled at each auger-hole. The composite samples were used in the laboratory for determining water content and chloride content, and for estimation of total soluble salts from 1:5 soil-water suspensions. The composite sample values were checked occasionally by determinations on replicate samples, specially retained for the purpose, and no statistically significant difference could be found between values for means of replicates and for composite samples. Similarly checks were made on soil paste conductances by comparing values obtained in the laboratory from composite samples with the mean values obtained in the field; again, no significant differences between the methods could be found.

The use of soil paste conductance as a guide to soil salinity has practical advantages inasmuch as the method is adapted to field conditions and is well established on that account (U.S. Dept. of Agriculture 1951). The relationship of soil salinity to conductivity is well known and has been considered recently in detail by Richards (1954). Some use is made of conductance values for conversion to proportions of soluble salts in the soil but the estimated concentrations are not accurate owing to variations in soils, composition of salts, and equipment. But although the soil paste conductance is not readily convertible to salt concentrations in the soil there is no doubt that the conductance does provide a useful measure of salt concentrations. Thus the same seasonal trend in salt concentrations is shown by the mean values of soil paste conductance and by determinations on 1:5 soil-water suspensions (Piper 1942).

The reason why the data on soil pastes are relied on for the main conclusions in this paper is that the individual results from replicate samples could be used to evaluate the statistical significance of mean values.

V. Results

(*a*) *Salinity*

Seasonal changes in salinity, as indicated by conductance determinations, are shown in Table 5 and in a series of graphs (Fig. 4). Mean

TABLE 5

SEASONAL CHANGE IN SOIL PASTE CONDUCTANCE IN PROFILES AT FIVE SITES, 1953-1954
Mean conductances of soil pastes from six replicates. Significant differences between consecutive means are indicated by S between the means (1% level of probability), and s between the means (5% level of probability)

Site	Sample	Texture	Depth (in.)	Conductance (mho × 10^4)						
				July 1953	Sept. 1953	Nov. 1953	Jan. 1954	Mar. 1954	Apr. 1954	July 1954
1A	1	Sand	0-1	0.16 S	0.49 S	8.4 S	55 S	50 S	4.3 S	0.98 S
	2	Sand	1-6	0.16 S	0.52 S	8.2 S	16 S	16 s	5.3 S	0.58 S
	3	Sand	12-14	0.51 S	2.7 S	14 S	18 S	10 S	12 S	6.9 S
	4	Sand	18-20	5.5 S	6.2 S	15 S	20 S	13 S	17 S	16 S
	5	SCL*	20-22	14 S	12 s	15 S	20 S	13 S	16 S	15 S
1B	1	Sand	0-1	0.12 s	0.41 S	0.38 S	6.1 S	7.3 S	1.2 S	0.20 S
	2	Sand	1-6	0.22 S	0.27 S	0.53 S	2.1 S	3.0 s	1.1 S	0.13 S
	3	Sand	12-14	0.36 S	0.72 S	3.1 S	3.2 S	2.3 S	1.2 S	0.33 S
	4	Sand	18-20	7.0 S	6.4 S	7.5 s	7.0 s	4.1 S	3.1 S	2.3 S
	5	SCL	32-34	14	13	14	14	11	9.0	8.1
1C	1	Sand	0-1	0.12 S	0.23 s	0.49 s	1.1 S	1.2 S	0.34 s	0.20
	2	Sand	1-6	0.12	0.15 s	0.39	0.48 s	0.79 S	0.25	0.20
	3	Sand	12-14	0.26 S	0.36 s	0.59 S	0.91 S	0.88 S	0.33 S	0.24
	4	Sand	24-26	0.91 S	0.92 s	4.2 S	3.8 S	2.7 s	0.94 S	0.33 S
	5	Sand	36-38	7.5 s	5.5 S	9.2	9.5	6.9	6.8	6.7 s
	6	SCL	44-46	11	10	14	13	10	8.7	8.7
2	1	Loam	0-1	0.66 S	4.1 S	12 s	23 s	20 S	3.2 s	1.7 S
	2	Clay	1-3	1.6 S	3.7 S	11 s	16 S	18 S	6.0 S	2.8 S
	3	Clay	7-9	9.5 s	6.6 S	12 S	18	18 s	20 S	9.4 S
	4	Clay	12-14	20 S	11 s	14 S	18	15 S	21 S	17
	5	Clay	18-20	24 S	14 S	14 S	17	14	15	18
	6	Clay	24-26	23 S	15	16	16	14	15 S	19

TABLE 5 (*Continued*)

Site	Sample	Texture	Depth (in.)	Conductance (mho × 10^4)						
				July 1953	Sept. 1953	Nov. 1953	Jan. 1954	Mar. 1954	Apr. 1954	July 1954
3	1	Sand	0-1	0.17 S	0.62 S	3.9 s	18 S	7.3 S	0.64 S	0.44
	2	Sand	1-6	0.38 S	0.72 S	4.1 s	4.5 S	2.3 S	1.2 S	0.43 S
	3	Clay	6-8	2.9 S	2.2 S	6.7 S	12 S	9.7 s	6.6 S	3.0 S
	4	Clay	18-20	11 S	5.3 S	14 S	15 S	13 S	15 s	10 S
	5	Clay	36-38	14 S	8.1 S	14 S	18 S	14 S	15	14

* Sandy clay loam.

determinations from six replicates, as recorded in Table 5, have been used in constructing the graphs, which show the change of conductance with sampling depth for each time of sampling and site. The results of determinations in the laboratory of total soluble salts from conductivities of 1 : 5 soil-water suspensions (Piper 1942) made from individual composite samples are given in Table 6. These results indicate the relative salt concentrations present at each sampled depth of soil and are useful for comparison with data on conductance of soil paste given in Table 5. It should be remembered that with high concentrations of salts the determinations are not a reliable guide to percentage salt content. Hence the values recorded for January and March at site 1*A* must be regarded with caution.

Determinations on composite samples at certain sampling dates, given in Table 7, indicate that chlorides make up the bulk of the salt content, which explains the marked seasonal changes in salt concentration.

Examination of the various tables and graphs mentioned above shows clearly that very marked changes occurred in soil salinity during the sampling period. The changes recorded at all sites follow a similar broad pattern but there are certain differences in emphasis and degree associated with particular profile features.

The most marked changes occurred in the surface horizons, particularly the top inch of soil. Salt contents of these layers increased from the first sampling in July 1953 and reached maximum values in January 1954. Decreased values were recorded following the opening rains in April, and by July 1954 values comparable with those of the previous July were recorded. The lower horizons did not exhibit such high seasonal variations and in some cases the salt contents remained constant throughout the year.

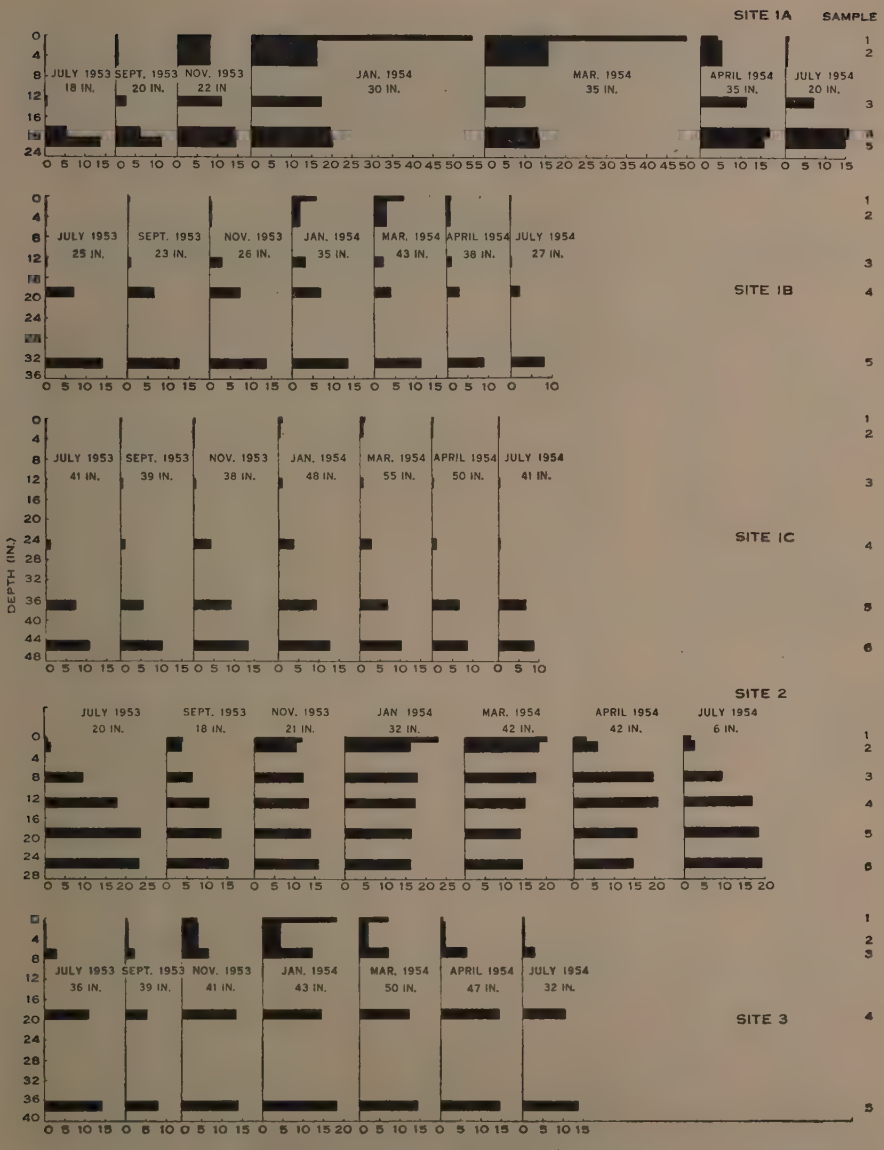

Fig. 4.—Seasonal changes in salinity on sites 1*A*, 1*B*, 1*C*, 2, and 3, as indicated by conductance determinations. Depths to ground-water are shown below sampling dates.

(*b*) *Moisture*

The percentage moisture content of each composite sample, together with the percentage moisture of certain horizons at 15 atm (pF 4.2),

are presented in Table 8. These pF values were determined on ground soil samples. The results show that: (i) the upper horizons were driest in January or March; (ii) there were big differences in water content between different sites and at different seasons; (iii) fine-textured subsoils remained relatively moist throughout the year.

TABLE 6

SEASONAL VARIATIONS IN SOIL SALINITY IN PROFILES AT FIVE SITES, 1953-1954

Salinity values estimated from composite of six replicates (375 × specific conductivity of 1 : 5 soil suspension at 20°C)

Site	Sample	Texture*	Depth (in.)	Total Soluble Salts (% oven-dry soil)						
				July 1953	Sept. 1953	Nov. 1953	Jan. 1954	Mar. 1954	Apr. 1954	July 1954
1*A*	1	S	0-1	0.03	0.04	0.35	2.9	4.3	0.25	0.08
	2	S	1-6	0.02	0.04	0.31	0.51	0.53	0.27	0.04
	3	S	12-14	0.02	0.13	0.42	0.68	0.36	0.50	0.27
	4	S	18-20	0.20	0.21	0.63	0.66	0.50	0.61	0.65
	5	SCL	20-22	0.51	0.58	0.56	0.62	0.55	0.74	0.72
1*B*	1	S	0-1	0.03	0.04	0.03	0.28	0.33	0.07	0.03
	2	S	1-6	0.02	0.02	0.03	0.06	0.13	0.05	0.03
	3	S	12-14	0.02	0.03	0.10	0.11	0.09	0.05	0.02
	4	S	18-20	0.20	0.24	0.23	0.27	0.15	0.13	0.10
	5	SCL	32-34	0.56	0.57	0.55	0.57	0.48	0.41	0.47
1*C*	1	S	0-1	0.02	0.03	0.02	0.04	0.04	0.03	0.03
	2	S	1-6	0.04	0.02	0.02	0.02	0.03	0.02	0.02
	3	S	12-14	0.01	0.02	0.02	0.03	0.04	0.02	0.02
	4	S	24-26	0.06	0.04	0.12	0.12	0.10	0.04	0.02
	5	S	36-38	0.17	0.13	0.37	0.32	0.24	0.28	0.34
	6	SCL	44-46	0.36	0.39	0.50	0.40	0.38	0.32	0.47
2	1	L	0-1	0.06	0.15	0.88	1.6	1.1	0.16	0.13
	2	C	1-3	0.17	0.28	0.59	0.99	0.99	0.43	0.25
	3	C	7-9	1.0	0.58	0.94	1.5	1.6	2.2	1.5
	4	C	12-14	1.5	0.84	0.73	1.0	0.89	1.4	1.8
	5	C	18-20	1.0	0.84	0.69	0.81	0.66	0.72	1.4
	6	C	24-26	0.83	1.0	0.89	0.89	0.81	0.70	1.1
3	1	S	0-1	0.04	0.05	0.20	0.54	0.38	0.04	0.04
	2	S	1-6	0.03	0.05	0.16	0.13	0.10	0.05	0.03
	3	C	6-8	0.14	0.20	0.29	0.48	0.60	0.37	0.16
	4	C	18-20	0.66	0.59	0.72	0.71	0.75	0.95	0.79
	5	C	36-38	0.72	0.95	0.74	1.2	0.90	0.98	0.88

* S, sand. SCL, sandy clay loam. L, loam. C, clay.

(*c*) *Ground-waters*

Determinations were made of the varying depth to ground-water, as shown in Figure 4, and of ground-water salinity. Seasonal variations in salinity are given in Table 9. The ionic composition of the various

ground-waters, sampled in July 1954, is given in Table 10. It should be mentioned that the determinations of depth to ground-water are only approximate, as the depth varied somewhat with lapse of time after opening a hole in the soil. In winter, free water may be found both in the

TABLE 7

VARIATIONS IN CHLORIDE CONTENT OF SOIL PROFILES, JANUARY-JULY 1954

Chloride values expressed as percentage of NaCl in composite soil samples

Site	Sample	Texture*	Depth (in.)	Chloride as NaCl (% oven-dry soil)			
				January	March	April	July
1*A*	1	S	0-1	1.9	3.2	0.12	0.019
	2	S	1-6	0.28	0.37	0.17	0.009
	3	S	12-14	0.39	0.22	0.34	0.15
	4	S	18-20	0.48	0.33	0.41	0.44
	5	SCL	20-22	0.36	0.36	0.51	0.44
1*B*	1	S	0-1	0.16	0.20	0.026	0.001
	2	S	1-6	0.034	0.064	0.020	0.001
	3	S	12-14	0.070	0.052	0.027	0.003
	4	S	18-20	0.18	0.085	0.079	0.048
	5	SCL	32-34	0.38	0.29	0.270	0.27
1*C*	1	S	0-1	0.011	0.008	0.004	0.003
	2	S	1-6	0.003	0.001	0.004	0.001
	3	S	12-14	0.013	0.010	0.007	0.001
	4	S	24-26	0.071	0.059	0.025	0.002
	5	S	36-38	0.21	0.14	0.19	0.22
	6	SCL	44-46	0.28	0.22	0.21	0.28
2	1	L	0-1	1.2	0.78	0.08	0.04
	2	C	1-3	0.65	0.63	0.28	0.11
	3	C	7-9	1.1	1.1	1.7	0.95
	4	C	12-14	0.79	0.56	1.1	1.3
	5	C	18-20	0.52	0.39	0.50	0.95
	6	C	24-26	0.59	0.50	0.49	0.77
3	1	S	0-1	0.36	0.21	0.01	0.002
	2	S	1-6	0.07	0.03	0.02	0.002
	3	C	6-8	0.32	0.33	0.23	0.093
	4	C	18-20	0.40	0.40	0.67	0.51
	5	C	36-38	0.80	0.52	0.67	0.57

* S, sand. SCL, sandy clay loam. L, loam. C, clay.

loose sand above the clay subsoils, on sites 1*A*, 1*B*, and 1*C*, and in marl below this subsoil. The ground-water levels for sites 1*A*, 1*B*, and 1*C* refer to water levels in the sand during the wetter months and to water levels in the marl during drier months. In other sites, the water levels all refer to levels in the deep marl.

All the water-tables were lower in summer; the lowest levels were recorded in March or April 1954. On all sites except site 2 the salinity of the ground-water was at a maximum in January and a minimum in July or September; at site 2 the maximum was in September and the minimum in March.

TABLE 8

SEASONAL VARIATIONS IN SOIL MOISTURE AT FIVE SITES, 1953-1954

Moisture values are composites of six replicates

Site	Sample	Texture*	Depth (in.)	% Water at pF 4.2†	Per Cent. Moisture						
					July 1953	Sept. 1953	Nov. 1953	Jan. 1954	Mar. 1954	Apr. 1954	July 1954
1*A*	1	S	0-1	2.1	13.4	16.4	17.0	10.7	9.2	10.0	17.1
	2	S	1-6		11.1	12.3	17.3	12.0	8.8	9.8	12.4
	3	S	12-14	0.7	13.7	15.7	14.3	15.8	11.5	12.7	15.9
	4	S	18-20		14.6	14.4	18.1	18.0	15.9	15.3	18.1
	5	SCL	20-22	8.0	16.9	18.5	17.7	17.2	17.0	18.3	18.5
1*B*	1	S	0-1		14	10.7	7.5	2.2	1.0	8.6	10.5
	2	S	1-6		10.4	8.4	9.1	6.3	4.2	7.1	10.5
	3	S	12-14		10.0	11.3	16.1	8.7	5.5	6.3	10.1
	4	S	18-20		14.9	15.9	15.8	13.8	8.3	10.3	16.2
	5	SCL	32-34		16.7	17.3	17.7	17.6	17.7	17.7	19.1
1*C*	1	S	0-1	1.9	11.9	5.0	1.8	0.3	0.4	7.4	11.5
	2	S	1-6		8.3	5.5	3.8	1.1	0.7	7.1	7.9
	3	S	12-14	0.6	6.9	4.0	5.1	2.9	2.0	4.7	6.5
	4	S	24-26		7.8	8.2	15.2	9.2	4.4	5.5	7.0
	5	S	36-38		11.9	10.8	18.5	16.9	11.8	13.7	16.5
	6	SCL	44-46	7.1	16.3	16.4	18.4	18.0	17.0	17.6	18.7
2	1	L	0-1	9.1	21.6	19.2	24.3	2.8	4.2	20.1	23.2
	2	C	1-3	23.1	33.8	15.9	35.7	20.0	17.4	26.0	32.3
	3	C	7-9	33.0	40.3	18.4	41.7	35.2	32.1	36.3	40.3
	4	C	12-14		33.7	31.1	30.3	28.4	21.8	28.7	36.8
	5	C	18-20		22.3	21.2	22.7	21.5	20.1	19.2	28.8
	6	C	24-26		23.1	25.1	27.5	23.9	25.2	20.6	30.6
3	1	S	0-1	1.4	18.9	17.5	13.1	0.6	0.3	11.4	15.5
	2	S	1-6		18.3	15.3	13.3	2.8	1.5	10.6	15.4
	3	C	6-8	13.5	19.8	20.8	22.3	15.5	17.4	20.6	22.6
	4	C	18-20		26.5	22.5	23.0	21.2	20.2	23.8	26.5
	5	C	36-38	24.4	21.9	24.5	20.4	29.4	22.2	26.2	23.6

* S, sand. SCL, sandy clay loam. L, loam. C, clay.

† Determinations of per cent. water at pF 4.2 were made by Dr. J. P. Quirk of the Division of Soils, C.S.I.R.O., Adelaide.

VI. Discussion and Conclusions

(*a*) *Salinity*

Soils with similar depths to ground-water and equally saline ground-waters but different profile features varied greatly in salinization. Sites 1*B*

and 2 were comparable in ground-water features but site 2 became more saline at the surface in summer, apparently owing to the greater opportunity for capillary movement of water in its predominantly clayey soil.

TABLE 9

SEASONAL VARIATIONS OF GROUND-WATER SALINITY

Total soluble salts expressed as parts per 1000; means of six replicates

Site	July 1953	Sept. 1953	Nov. 1953	Jan. 1954	Mar. 1954	Apr. 1954	July 1954	Min. Sig. Diff.*
1*A*	21	15	27	33	25	22	25	6
1*B*	15	15	22	29	26	19	10	6
1*C*	19	9	16	20	15	14	13	8
2	26	32	26	27	18	19	22	6
3	20	23	32	37	33	27	24	4

* $P = 0.01$.

Sites 1*A*, 1*B*, and 1*C* differed from each other not only in soil morphology but also in depth to ground-water. Sites 1*A* and 1*C* also had different plant covers and ground-water salinities. The maximum percentage of chlorides as NaCl in the surface inch of sites 1*A*, 1*B*, and 1*C* were respectively 3, 0.2, and 0.01, and this variation was no doubt due to several factors. Water movement to the surface would be affected by the different depths of sand, vegetative cover, and depth to ground-water,

TABLE 10

COMPOSITION OF GROUND-WATERS (M-EQUIV. PER L.)

Sampled in July 1954

Site	Na	K	Ca	Mg	Cl	HCO_3	SO_4
1*A*	330	4.3	9.5	58	300	21	27
1*C*	285	5.2	9.5	59	280	25	
2	345	7.6	7.0	107	402	13	35
3	370	6.0	4.0	100	394	18	33

while a greater accumulation of salts would have been expected in site 1*A* merely because of the differences in ground-water salinity. The difference in maximum salt concentrations between sites 1*B* and 1*C* was apparently due to a difference of about 14 in. in depth of sand, a corresponding difference in ground-water depth, and a greater degree of plant cover on site 1*C*.

Sites 1*C* and 3 were comparable in depth of ground-water but differed in soil morphology, ground-water salinity, and plant cover. The finer-textured profile of site 3, together with a more saline ground-water and lack of plant cover, resulted in a maximum surface chloride concentration of 0.36 per cent. (as NaCl) as against 0.01 per cent. for site 1*C*.

The differing salt concentrations at the various sites result from features such as:

(i) Differences in soil morphology,
(ii) Varying depths to ground-water,
(iii) Different ground-water salinities,
(iv) Differing densities and species of plants growing on the sites.

(*b*) *Soil Moisture Changes*

The soil moisture results can be considered either in relation to salinity changes or for their information on the type of moisture movement and moisture availability to plants in soils with shallow ground-water. The highest surface salt concentrations occurred at site 1*A*, and results at this site also show fairly high moisture levels throughout the year. On the other hand at site 1*C*, with the lowest salt concentrations at the surface, the soil down to 14 in. had dried out to less than 5 per cent. moisture in the November-March period. Comparatively high moisture contents were maintained in the saline sites 1*B*, 2, and 3.

The maximum salt concentrations at the surface were recorded for most sites in January and hence capillary movement apparently has occurred in soils with moisture contents at the November level. It is conceivable that capillary movement still occurred under the soil moisture conditions determined in January, but this cannot be demonstrated from the salinity determinations recorded in March. Taking the November soil moisture levels as being associated with capillary movement, it is noticeable for site 1*C* that water movements occurred at moisture contents at or below wilting point. After capillary movement of water to the surface ceased in the January to March period, further drying of the soil was caused by plants, especially the lucerne on site 1*C*.

(*c*) *The Relationship of Salinity Distribution and Climate*

Rainfall leaches salts down the soil profile, even as far as the ground-water, with a compensating upward movement as a result of capillary action. Relevant meteorological data involving rainfall records and saturation deficit values for the 12 months are presented in Table 11; these show that maximum saturation deficit and minimum rainfall corresponded with the period of greatest surface salt concentration.

During this period as a result of water loss, by either capillary action, consumption by plants, or other means, the retreat of ground-water resulted in the surface soils becoming separated from the capillary fringe. This appears to be the main factor in the general lack of increased salinity in the surface inch from January to March. However, on site 1*A* where the surface did not become separated from the capillary fringe, the chloride values from Table 7 indicate that salts did continue to accumulate in the surface between January and March.

In the March-April period the lower temperatures, and consequently lower saturation deficits, coincided with the commencement of winter rains. These conditions resulted in lower salt contents in all surface soils at the April sampling. This reduction, occurring after 3.47 in. of rain, virtually cleared the salts from the sandy upper horizons, except on site 1*A*. Reductions of surface salinity were accompanied by increased salinities in lower horizons and it is evident from determinations in 1953 that extensive leaching of the soil by winter and spring rains is required to give minimum salt concentrations in these lower horizons.

TABLE 11

METEOROLOGICAL DATA FOR TINTINARA AND KEITH, 1953-1954

Pre-sampling Period	Total Rainfall (in.)	No. of Rainfall Days	Rainfall (in./rain day)	Dry Bulb Temp., 9 a.m. (°F)	Wet Bulb Temp., 9 a.m. (°F)	Relative Humidity (%)	Satur'n. Deficit (in. Hg)
1.vi.1953-23.vii.1953	6.69	28	0.24	49	45	71	0.10
24.vii.1953-17.ix.1953	4.28	26	0.16	52	49	79	0.08
18.ix.1953-12.xi.1953	4.59	20	0.23	60	53	60	0.21
13.xi.1953-11.i.1954	2.08	7	0.29	69	58	47	0.38
12.i.1954-8.iii.1954	0.96	5	0.19	71	60	49	0.39
9.iii.1954-26.iv.1954	3.47	7	0.49	64	57	62	0.23
27.iv.1954-20.vii.1954	5.63	34	0.17	52	49	79	0.08

(*d*) *Agronomic Implications*

(i) The use of single determinations of soil salinity for characterization of the soils is of very limited value in areas with shallow saline groundwater, as seasonal changes are likely to be large. Salinity determinations for such soils are of little value if no mention is made of the season of sampling. It is noticeable that the chloride content at the surface of any site was below 0.04 per cent. NaCl in July 1954, yet previously the concentrations had varied from 0.04 to 3.2 per cent., depending on the site chosen. If the seasonal range of salinity cannot be given it is important to record information on the depth and salinity of the ground-water in conjunction with soil salinity data. It is preferable to record the salinity in midsummer as the maximum salinity likely to occur, since this together with ground-water information will indicate how serious the salinity is likely to be. It is advisable in saline areas to obtain more than one sample to characterize an area; samples spaced laterally and vertically should be obtained.

(ii) The occurrence of saline ground-water, containing more than 1.5 per cent. total soluble salts at depths not greater than 48 in. in summer, was found to be associated with failure of economic pasture plants commonly used in southern South Australia, viz. lucerne, subterranean clover, and *Phalaris tuberosa*. In winter the saline ground-water occurred within 36 in. of the surface on sites where such failure was noticed. On site 1*C*, where the ground-water was never within 36 in. of the surface, lucerne and other pasture plants have been maintained for 5 years, and salt accumulation at the surface was found to be almost insignificant. The soil profile and ground-water salinity also have been found to influence seasonal salt concentrations. Capillary movement was found to be quite marked through a thickness of 3 ft of sand in site 1*B*, but almost insignificant through 4 ft of sand.

(iii) The annual grasses found on the cultivated sites may grow in moderately saline areas, either because of physiological adaptation to the higher salt concentrations, or because their growing season is sufficiently short to escape the more saline conditions in the autumn or late spring. Coast barb grass, *Polypogon maritimus*, and stinkwort have some capacity for growth in moderately saline conditions. Only isolated plants of Wimmera ryegrass, *Phalaris tuberosa*, cape-weed, subterranean clover, cereal barley, or strawberry clover were noticed on sites 1*A*, 1*B*, and 3, which appear to have been far too saline for productive pasture plants.

(iv) The growth of lucerne on site 1*C* strongly suggests that it makes use in summer of ground-waters containing more than 1.5 per cent. total soluble salts, or more than 1000 gr/gal. This water is much more saline than water usually regarded as suitable for irrigating lucerne. In South Australia, the widely supported recommendation of Ward (1946) on classification of waters for irrigation gives the upper limit of salinity in water for lucerne as 210 gr/gal total soluble salts. However, several cases are known in the Murray Mallee where water for lucerne irrigation contains from 210 to nearly 500 gr/gal (Barnes 1951). It is possible that under the conditions of site 1*C* the lucerne was able to make some use of the saline ground-water but would not depend on it so much as in the low-rainfall areas referred to above where mean rainfall for the 6 months, November to April, is approximately 4 in., compared with 6 in. at Tintinara.

The failure of lucerne on sites 1*A* and 1*B* is due partly to the excessive salinity throughout the profiles in summer and partly to waterlogging in winter.

(v) The moisture results have application to other, non-saline areas in the Coonalpyn Downs where the soils consist of variable depths of loose sand over a relatively dense, level subsoil. In such soils a perched water-table is maintained temporarily above this subsoil in winter and spring. The moisture results obtained at sites 1*B* and 1*C* suggest that annual shallow-rooting plants such as subterranean clover are able to

make use of this water when it rises by capillary movement in late spring. This effect is likely to occur in soils with 3 ft of sand over a clay subsoil and probably with 4 ft of sand over clay.

(vi) A further application of these results is to those soils which, although detached from permanent ground-water, may contain appreciable amounts of soluble salts in the deeper subsoils. Many such soils are subject to temporary waterlogging, and it is likely that capillary movement in some of these soils will bring concentrations of salts to the surface in late spring and early summer. It is unlikely that these conditions would occur except in cleared, heavily grazed, and compacted soils.

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COPPER-MOLYBDENUM-SULPHATE INTERACTION IN INDUCTION OF OVINE HYPOCUPRAEMIA AND HYPOCUPROSIS

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(*Manuscript received July* 6, 1955)

Summary

A basal diet containing 5.2 p.p.m. copper, 0.8 p.p.m. molybdenum, and 0.04 per cent. inorganic sulphate was fed unsupplemented to one group of sheep. Four other groups were fed on the same diet supplemented with ammonium molybdate to give a molybdenum content of 5.1 p.p.m. or with sodium sulphate to give an inorganic sulphate content of 0.40 per cent., or with both.

Sheep on the unsupplemented basal diet showed no marked disturbance of their liver and blood copper concentrations.

Sheep maintained for 50 weeks on the diet containing both molybdenum and sulphate supplements showed a progressive fall in liver and blood copper levels, and developed dystrophic wool and hypochromatrichia. On a restricted feed intake of the same diet, sheep displayed a similar fall in liver copper and similar wool changes, but maintained a normal blood copper level for a longer period before developing hypocupraemia. Hypochromatrichia appeared to develop in this group before hypocupraemia was evident.

With only the sulphate supplement added to the basal diet, liver copper concentrations fell, but not to a level associated with hypocupraemia.

With only the molybdenum supplement added to the basal diet, copper retention by the liver was depressed to a small, but significant extent compared with the controls.

The diet of the groups showing evidence of hypocuprosis approximately reproduced the mean copper, molybdenum, and sulphate status of the feed in an area in New South Wales enzootically affected with hypocuprosis. It is concluded that hypocuprosis in this area at least is explicable in terms of copper-molybdenum-sulphate interaction.

I. INTRODUCTION

No consistent relationship has been found between pasture copper levels and incidence of ovine hypocuprosis. For example, Allcroft (1952) has recorded ovine hypocuprosis in the United Kingdom on pastures containing 7-20 p.p.m. of copper, and at the other extreme, Beck (1941) has associated hypocuprosis in Western Australia with pasture containing less than 3-5 p.p.m. of copper. Dick and Bull (1945) showed that dietary molybdenum reduced the liver copper level of sheep. As a consequence there arose a concept of a "simple" copper deficiency occurring on pastures containing less than 3 p.p.m. of copper, and a "conditioned" or "complicated" copper deficiency caused by the combination of a moderately

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high molybdenum and a normal copper content in the pasture (Dick and Bull 1945; Cunningham 1946, 1949). This concept appeared valid in some areas, but notably not in the United Kingdom, where it was considered quite inadequate (Stewart, Farmer, and Mitchell 1946; Green 1951). Following the recognition of the importance of sulphate in governing the effect of molybdenum on copper metabolism (Dick 1953*a*) it was suggested (Dick 1953*b*) that this disparity in findings could be explained by variations in the sulphate content of the feed.

An experiment designed to investigate Dick's suggestion, and also to study the interaction between plane of nutrition and induction of hypocuprosis, is now reported. The copper, molybdenum, and sulphate concentrations in one of the diets reproduced the average levels found in the pastures of an area in the Central Western Slopes of New South Wales enzootically affected with ovine hypocuprosis as evidenced by white banding in black wool, dystrophic ("steely") wool, and enzootic ataxia. The symptoms have been associated with liver copper values below 20 p.p.m. and blood copper values below 0.05 mg/100 ml.

The results of the experiment have confirmed Dick's (1953*b*) hypothesis.

A preliminary account of some aspects of this experiment has already been published (Wynne and McClymont 1955).

II. Experimental

Thirty-two Merino weaners and wethers, including 10 black sheep, were divided into five groups of six or seven sheep on a basis of body weight, age, liver copper level, and colour of wool, some black sheep being included in each group. Each group was housed in a separate pen and fed as follows:

Group 1.—Basal diet, *ad lib.*

Group 2.—Basal diet plus molybdenum and sulphate supplements, *ad lib.*

Group 3.—Diet as for group 2 but on a restricted ration of 2.7 kg per head per week, fed as 1.35 kg per head on Mondays and Thursdays.

Group 4.—Basal diet plus molybdenum supplement, *ad lib.*

Group 5.—Basal diet plus sulphate supplement, *ad lib.*

The percentage composition of the basal diet was as follows: chaffed wheaten or oaten hay, 40; oats, 30; wheat, 23½; meatmeal, 5; urea, ¾; limestone, ½; salt, ¼. The diet included cobalt supplements to increase the cobalt content of the diet by 0.1 p.p.m., and intermittent massive vitamin A supplements. Estimated crude protein content, 12 per cent.

Each batch of the major constituents of the diet was sampled for analysis for copper, molybdenum, and inorganic sulphate. The mean values were used to calculate the mean composition of the basal diet (Table 1).

The diets of groups 2, 3, and 4 were supplemented with 0.720 g ammonium molybdate ($(NH_4)_6Mo_7O_{24}.4H_2O$) per 91 kg (200 lb) of basal ration, which increased the molybdenum content of the diet by 4.31 p.p.m. to 5.14 p.p.m.

TABLE 1

ANALYSIS OF BASAL DIET

Data shown as mean and standard error of determinations on batches of feed constituents

Feed	Copper (p.p.m.)	Molybdenum (p.p.m.)	Inorganic Sulphate (% SO_4)
Cereal chaff	4.7 ± 0.7	1.07 ± 0.11	0.07 ± 0.01
Oats	4.5 ± 0.5	0.80 ± 0.15	0.00
Wheat	3.7 ± 0.5	0.45 ± 0.05	0.00
Meatmeal	20.7 ± 0.5	1.10 ± 0.14	0.22 ± 0.02
Basal diet*	5.2 ± 0.6	0.83 ± 0.11	0.04 ± 0.005

* Calculated from analyses of constituents.

The diets of groups 2, 3, and 5 were supplemented with 1100 g sodium sulphate decahydrate ($Na_2SO_4.10H_2O$) per 91 kg of feed, which increased the sulphate content of the diet by 0.36 per cent. to 0.40 per cent.

The ammonium molybdate, dissolved in about 500 ml of water, was added to the feed during mixing. The sodium sulphate was finely ground from clean crystals of the decahydrate and added to the ration during mixing. The copper, molybdenum, and sulphate contents of the diets are recorded in Table 2.

TABLE 2

COMPOSITION OF DIETS AND LIVER COPPER CONCENTRATIONS

Group	Composition of Diet			Sheep No.	Liver Copper (p.p.m. dry wt.)			
	Cu (p.p.m.)	Mo (p.p.m.)	SO_4 (%)		Pre-expt.	At 17 Weeks	At 30 Weeks	At 50 Weeks
1	5.2	0.83	0.04	B43	110	105	295	
				B44	350	205		
				B46	280	145	295	
				B61	150	34	105	
				B62	400	380		
				B75	235	145	250	
				Mean	254	169	236	
2	5.2	5.14	0.40	B38	73	20	14	8
				B41	230	56	35	17
				B49	220	35	29	21
				B57	230	115		
				B66	250	46	28	15
				B72	290	23	22	9
				B81	260	19	21	7
				Mean	222	44.9	24.8	12.8

TABLE 2 (*Continued*)

Group	Composition of Diet			Sheep No.	Liver Copper (p.p.m. dry wt.)			
	Cu (p.p.m.)	Mo (p.p.m.)	SO_4 (%)		Pre-expt.	At 17 Weeks	At 30 Weeks	At 50 Weeks
3	5.2	5.14	0.40	B40	100	7	10	8
				B50	140	23	16	11
				B70	180	18	18	7
				B79	235	37		
				B80	180	38	22	11
				B83	385	110	29	9
				Mean	203	38.8	19.0	9.0
4	5.2	5.14	0.04	B45	290	130	120	
				B48	310	245	230	
				B63	150	100	92	
				B65	415	305	270	
				B69	335	165	200	
				B73	425	225	160	
				B82	220	99	120	
				Mean	306	181	170	
5	5.2	0.83	0.40	B39	140	43	53	63
				B42	370	120	130	50
				B60	175	91	11	15
				B64	225	96		
				B74	340	160	140	105
				B78	130	50	16	16
				Mean	230	93.3	70.0	49.8

Results of analyses of covariance

Group	Adjusted Mean Fall in Liver Copper Concentration (p.p.m.)		
	17 Weeks	30 Weeks	50 Weeks
1	81	−8	
2	188	210	230
3	184	210	232
4	96	94	
5	144	170	194
Approx. sig. diff. ($P = 0.05$)	55	60	28

Liver samples for copper analysis were taken by biopsy (Dick 1952) at the commencement, and at intervals during the experiment. Blood samples for copper were taken on three occasions.

All sheep were weighed every 3 weeks and examined for changes in the wool. All sheep were shorn 4 weeks after the commencement of the experiment.

After 36 weeks, groups 1 and 4 were discontinued because the results indicated that no further changes were likely to occur in these groups.

Copper was determined in feed samples, livers, and bloods by the method of Clare, Cunningham, and Perrin (1945). The method of Perrin (1946) was used for molybdenum with some modifications (Dick and Bingley 1951). The modifications were the incorporation of a sodium fluoride reagent and an extra washing of the amyl alcohol layer with stannous chloride solution.

Inorganic sulphate was estimated by a provisional method which is still subject to revision. Briefly, the method used was as follows:

A 3 g sample of finely ground feed was treated with 5 ml ferric chloride solution (50 g $FeCl_3.6H_2O$ made up to 100 ml with distilled water) and 42 ml distilled water. The mixture was brought to the boil. When cool, 3 ml ammonium hydroxide (50 per cent. v/v) was added, and the mixture stirred and then allowed to stand for at least 10 min. The mixture was filtered, and an aliquot of the filtrate analysed for sulphate by the turbidometric method of Steinbergs (1953). The optical density of the barium sulphate suspensions was measured on a spectrophotometer at 400 mμ using individual blanks to zero the instrument for each determination. The sulphate content was calculated by reference to a standard graph.

III. Results

(*a*) *Liver Copper*

Changes in liver copper concentrations during the experiment are recorded in Table 2. Total liver copper contents at times of sampling were estimated on the basis of liver weight being 1.5 per cent. of body weight. Values are recorded in Table 3.

The mean liver copper concentration of the control group (group 1) had fallen somewhat at 17 weeks, but at 30 weeks, in three of the four survivors the concentrations had increased to above the pre-experimental levels (some sheep were lost owing to an obscure infection following biopsy). The estimated total liver copper did not show this drop, the values being similar at 0 and 17 weeks. It seems likely that the initial drop in liver copper concentration was the result of increase in size of the liver following the rapid growth on transfer from poor pasture to the high protein diet fed *ad lib.* However, all four survivors in this group showed considerable gain in calculated total liver copper by 30 weeks, indicating that, for some reason not apparent, efficiency of copper retention had improved between 17 and 30 weeks. The mean liver copper levels of the sulphate-molybdenum supplemented sheep, groups 2 and 3, progressively fell over 50 weeks to 12.8 and 9.0 p.p.m., all sheep being very uniformly affected. The mean liver copper of the sulphate supplemented group (group 5) decreased over the same period to 49.8 p.p.m. with considerable variation between sheep. With the molybdenum supplemented sheep (group 4) the liver copper concentration fell only slightly

TABLE 4

BLOOD COPPER LEVELS AND INCIDENCE OF WOOL CHANGES

Group	Sheep No. and Colour	Blood Copper* (mg/100 ml) At 15 Weeks	At 30 Weeks	At 43 Weeks	Wool Change and Time of Incidence
1	B43 Black	0.08	0.11		No change
	B44 White	0.14	†		
	B46 White	0.11	0.09		No change
	B61 White	0.12	0.11		No change
	B62 White	0.09	†		
	B75 White	0.11	0.10		No change
	Mean	0.108	0.103		
2	B38 Black	0.03	0.03	0.05	Light band, 13th week
	B41 Black	0.09	0.06	0.03	Light band, 30th week
	B49 White	0.05	0.05	0.05	Dystrophy, 50th week
	B57 White	0.05	†		
	B66 White	0.07	0.04	0.02	Dystrophy, 30th week
	B72 White	0.08	0.06	0.05	Dystrophy, 30th week
	B81 Black	0.08	0.05	0.05	Light band, 17th week
	Mean	0.064	0.048	0.042	
3	B40 Black	0.10	0.04	0.03	Light band, 13th week
	B50 White	0.08	0.13	0.04	Dystrophy, 30th week
	B70 White	0.09	0.06	0.02	No change
	B79 White	0.10	†		
	B80 Black	0.07	0.04	0.04	Light band, 15th week
	B83 Black	0.10	0.08	0.04	Light band, 30th week
	Mean	0.090	0.070	0.034	
4	B45 White	0.17	0.09		No change
	B48 White	0.12	0.10		No change
	B63 White	0.11	0.09		No change
	B65 White	0.08	0.08		No change
	B69 White	0.11	0.07		No change
	B73 White	0.12	0.09		No change
	B82 Black	0.11	0.08		No change
	Mean	0.117	0.086		
5	B39 Black	0.09	0.10	0.07	No change
	B42 Black	0.08	0.08	0.08	No change
	B60 White	0.07	0.05	0.07	No change
	B64 White	0.09	†		
	B74 White	0.09	0.07	0.08	No change
	B78 White	0.10	0.07	0.09	No change
	Mean	0.087	0.074	0.078	

* Min. sig. diff. between mean blood copper levels ($P = 0.05$): at 15 weeks, 0.023; at 30 weeks, 0.025; at 43 weeks, 0.014.

† Died at 17 weeks.

on the restricted intake of the sulphate-molybdenum supplemented diet, the mean blood copper did not fall below 0.07 mg/100 ml until after the 30th week. At 15 weeks the difference between the mean blood copper values of the *ad lib.* and restricted groups, 0.064 and 0.090 mg/100 ml respectively, was significant.

The mean blood copper level of the sheep on the sulphate supplemented diet (group 5) fell significantly below that of the control at 30 weeks but did not fall further to the low levels recorded in the sulphate-molybdenum supplemented groups. There was no significant difference between the blood copper levels of the controls and the sheep on the molybdenum supplemented diet (group 4).

At 57 weeks (not recorded in the table), the mean blood copper levels of the sulphate-molybdenum supplemented groups had both fallen to 0.030 mg/100 ml.

TABLE 5

WEIGHT GAINS AND FOOD CONSUMPTION OF SHEEP ON DIFFERENT DIETS*

Treatment	Mean Initial Weight (kg)	Mean Final Weight (kg)		Mean Rate of Gain† (kg/day)		Mean Food Consumption per Head (kg/day)
		At 36 Weeks	At 50 Weeks	At 36 Weeks	At 50 Weeks	
1	22.5	34.7	—	0.052	—	0.83
2	23.8	36.7	40.5	0.057	0.052	0.79
3	23.1	28.8	28.9	0.029	0.021	0.51
4	21.5	37.4	—	0.064	—	0.78
5	27.8	39.2	42.4	0.053	0.047	0.78

* Based on survivors.

† Includes corrections for shearing.

(*c*) *Wool Changes*

All sheep in groups 1, 4, and 5 grew normal wool. In contrast, the wool of all except one of the surviving sheep in the sulphate-molybdenum supplemented groups (2 and 3) showed characteristic evidence of hypocuprosis. Hypochromatrichia occurred in the wool of the six black sheep in these groups, showing as grey bands which in the length of the staple tended to become wider, with eventual almost complete disappearance of pigmentation. Typical examples are shown in Plate 1. However, some banding persisted throughout the experiment and bands of normal pigmentation occurred even late in the experiment after a considerable length of very pale wool had grown, as shown in the wool of the sheep B80 in Plate 1. There was also a considerable variation in the time before banding occurred. The time at which wool abnormality was first noted is recorded in Table 4.

Wool changes in the white sheep consisted of decreased crimp definition and, in some sheep, definite secondary waves. In sheep B66 (Plate 1),

cessation of secondary waves with improvement of crimp definition, similar to the return of normally pigmented wool in sheep B80, occurred towards the end of the experiment.

(*d*) *Growth and Feed Consumption*

There was no significant difference in weight gain and no appreciable difference in food consumption between the groups on the unrestricted diets (Table 5), indicating that appetite and growth are not necessarily depressed by a degree of hypocuprosis which is sufficient to affect the wool. Group 3, on half to two-thirds of the *ad lib.* food intake, gained about one-half of the weight gained by the other groups.

IV. Discussion

It has been clearly demonstrated that, with the basal diet used, supplementation with molybdenum and sulphate resulted in a hypocuprosis characterized by low liver copper values, hypocupraemia, hypochromatrichia, and dystrophic wool. This finding has the added significance that the levels of copper, molybdenum, and sulphate in the experimental diet were of the same order as those found in the natural feed of sheep in an area of enzootic hypocuprosis. Thus it appears likely that the hypocuprosis of that area, and no doubt of others, can be explained in terms of the copper, molybdenum, and inorganic sulphate contents of the feed. However, it cannot, of course, be assumed that unknown factors in the basal diet were not involved in these experiments or that unknown factors do not operate in the field.

The experiment has confirmed the suggestion put forward by Dick (1953*b*) that sulphate could be a factor in the induction of ovine hypocuprosis under natural conditions.

The production of low liver copper and depressed blood copper levels on a diet containing about 0.8 p.p.m. of molybdenum and 0.4 per cent. of inorganic sulphate (group 5) suggests that hypocuprosis could be associated with molybdenum levels of the order of 1 p.p.m. in the feed provided the inorganic sulphate intake is high (see Dick 1953*b*). This has some relevance to the hypocuprosis problem in the United Kingdom, where some enzootic swayback pastures are reported to contain 0.3-1.2 p.p.m. of molybdenum (Stewart, Farmer, and Mitchell 1946).

Restriction of the feed intake, and consequent restriction of the ingested copper, molybdenum, and sulphate, did not affect the fall in liver copper concentration and the induction of signs of hypocuprosis (group 3) in the fleece. It appears, then, that the *concentrations* of copper, molybdenum, and sulphate in the diet are of more importance in copper metabolism than the *absolute intakes* of the three factors. It was of interest, however, that the sheep on the low plane of nutrition maintained normal blood copper levels at a time (15 weeks) when their mean liver

copper concentrations would have been lower than that of the sheep on the unrestricted intake which were showing hypocupraemia. They also apparently showed signs of hypocuprosis before hypocupraemia developed. This is an association which we have observed in the field and which stimulated our interest in the interaction of plane of nutrition and copper metabolism. Dick (1954) has reported the induction of dystrophic wool without hypocupraemia with sheep receiving very large supplements of molybdenum and sulphate and having normal liver copper values.

The wool changes observed in the experiment were in accordance with the sequence reported to occur with increasing hypocuprosis in field observations and experiments, viz. hypochromatrichia of black wool (H. B. Carter, personal communication), loss of crimp definition, and superimposition of secondary waves on the deteriorating crimp (Marston and Lee 1948). The wool changes did not reach the stage of complete disappearance of the normal crimp, in accordance with the observation of the latter workers that this did not occur until the blood copper level had fallen below 0.02 mg per cent.

The intermittent return of pigmentation in the black wool and the return of normal crimping as shown in sheep B66 (Plate 1) cannot be explained. It indicates, however, that the banding of black wool in the field is not necessarily a reflection of variations in intake of dietary factors.

Further work is needed to define more closely the relations between copper, molybdenum, and sulphate as regards their effect in inducing hypocuprosis. But it is quite evident that interdistrict and interseasonal differences in the incidence of hypocuprosis are probably explicable, at least in part, by variations in the copper, molybdenum, and sulphate contents of the ingested feed and, particularly, in the duration of time over which the intake of these factors is such as to result in an appreciable rate of loss of liver copper. Such variations would in turn depend on soil type, climatic conditions, species and stage and rate of growth of the pasture plants, and fertilizer treatments.

V. Acknowledgments

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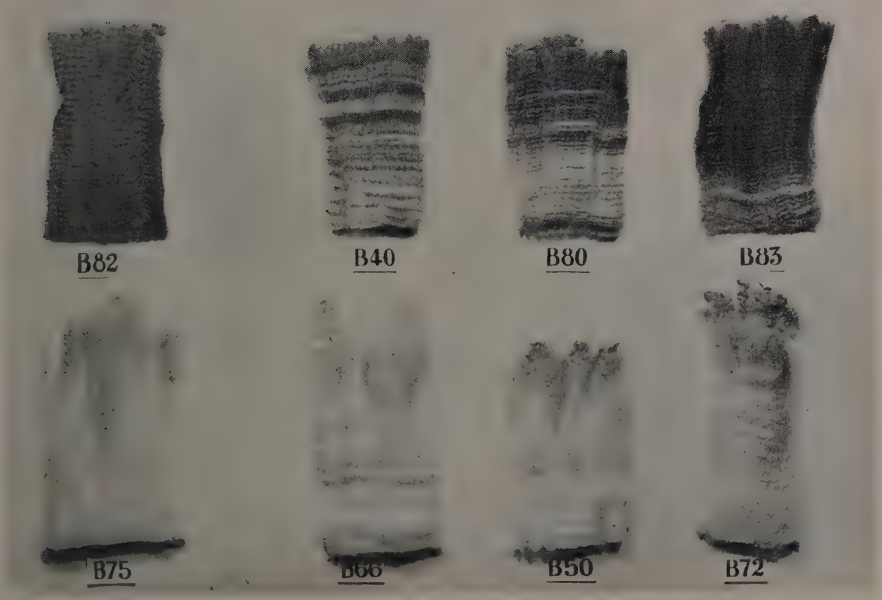
INDUCTION OF OVINE HYPOCUPROSIS



Wool from normal and hypocuprotic sheep.

Two typical normal black and white wools from sheep in groups 4 and 1 respectively are shown on the left. The other samples are from sheep on the sulphate-molybdenum supplemented diets, showing banding of black wool, loss of definition of crimp, and in some, occurrence of secondary waves.

BODY-WEIGHT–FLEECE-WEIGHT RELATIONSHIPS IN A STRAIN OF MERINO SHEEP

By P. G. SCHINCKEL*

(*Manuscript received July* 18, 1955)

Summary

The relationship of body weight to wool production was examined in a flock of Merino sheep of South Australian strain over a period of 7 years.

In only one out of 10 groups examined was there a significant correlation between body weight and the amount of clean wool produced per unit area of midside skin. It is concluded that body weight and wool production per unit area of body surface are independent. In all groups there was a highly significant correlation between clean fleece weight and clean wool per unit area of body surface in the midside region.

The regression of log fleece weight on log body weight was determined in 15 groups. In no case was the regression coefficient significantly different from 0.60. As the regression of log surface area on log body weight in sheep is of the order of 0.60, it is concluded that wool production is proportional to fleece-bearing surface. The mean regression coefficients of log fleece weight on log body weight, calculated within sire and year groups, were: rams, 0.52 $\pm$ 0.056; ewes, 0.61 $\pm$ 0.038; wethers, 0.50 $\pm$ 0.068. There were no significant differences between sires in the regression of log fleece weight on log body weight. There were, however, highly significant differences between sire groups in mean log fleece weight, after adjustment for differences in log body weight.

Skin areas 3 by 3 cm were tattooed on the left midside of 24 lambs at 1 month of age. The wool produced on these areas, and the areas of the tattoos, were measured at 4-monthly intervals from 4 months of age until 28 months. The amount of wool produced was proportional to the area in each of the six periods. There was also a highly significant difference between periods and between sheep in the amount of wool produced after adjustment for differences in tattoo area.

I. INTRODUCTION

There are numerous reports in the literature of a significant correlation between body weight and wool production in sheep (Duerden, Murray, and Botha 1932; Johansson and Berge 1939; Terrill and Stoehr 1942; Pohle and Keller 1943; Jones *et al.* 1944; Slen, Peters, and Myhr 1954). Working with a strain of Australian Merino sheep, Morley (1955), and Morley, Lockart, and Davis (1955) found a significant correlation between body weight and total raw wool production, but correlations between body weight and wool production per unit area of skin were not significant (Morley, Lockart, and Davis 1955).

Galpin (1947) observed the wool production of Romney Marsh sheep at Cambridge in different seasons of the year. She reported that, in periods when feed supply was good, "all the sheep . . . produced approxi-

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mately the same weight of wool per day per sq. cm. of hip region skin". She further states that "it is therefore possible to say that in these experiments with this flock each sheep appears to have a maximum hip region wool production (per unit area), . . . which is the same for every sheep in the flock". Galpin also observed differences in wool production per unit area of skin in different regions of the body and concluded that differences in total wool production resulted from differences in total surface area and from different proportions of high- and low-producing body regions.

Henderson (1953) observed the regional and total wool production of Romney Marsh sheep from birth to 12 months of age on different planes of nutrition and found a close relationship between amount of wool produced and estimated surface area.

The object of the examinations reported here was to study the relationship of clean wool production to body weight in a flock of sheep of normal genetic diversity and to determine whether wool production varied *pari passu* with smooth body area, itself a function of body weight. A correlation between fleece weight and body weight does not necessarily mean direct proportionality of wool production and surface area.

The observations followed along two lines: firstly, a statistical analysis of the relationship between wool production and body weight in sheep run under good husbandry conditions; and secondly, observations on the wool production in early adult life of skin areas permanently identified by means of tattoo lines soon after birth.

II. Materials and Methods

The relationship of skin area to body weight is a particular case of the general equation of allometry, and takes the form

$$A = KM^x$$

whence

$$\log A = \log K + x \log M,$$

where A = skin area, M = body weight, and K is a constant.

In the arithmetic form, x is the power to which weight is raised in area-weight relationships, while in the logarithmic form it is the regression coefficient of log A on log M. No measures of surface area were made on the sheep in these observations and it was therefore necessary to approach the problem indirectly by means of the regression of log fleece weight on log body weight. Agreement between this regression coefficient and that of log surface area on log body weight determined in other observations may reasonably be interpreted as indicating a direct relationship between surface area and clean wool production.

Not all the skin surface is wool-bearing; and we are aware neither of any reliable estimates of the wool-bearing surface as a proportion of

the whole, nor of the variation which may occur between animals in this respect. It is considered that the possible errors associated with failure to take these variables into account are unlikely to affect seriously the value of the regression coefficients, although they will almost certainly affect the value of the standard errors of these coefficients. Similar conclusions apply to the effect of skin folding on skin area. Unpublished observations from this flock indicate that the limited range of skin folds present (the South Australian Merino is relatively free of skin folds) is positively associated with clean wool production but not with body weight. Morley (1955) has recorded similar relationships. The effect of not taking this factor into account therefore will be to increase the standard errors of the regression coefficient but not to alter the absolute value of these coefficients.

The animals on which these observations were made were run under field conditions in which no measure of feed intake was possible. In order to reduce possible errors from this source the analyses were made on a within year and sex basis. All animals within a group were thus exposed to a common nutritional and climatic environment. These observations are therefore subject to the qualification that they are made on sheep of normal genetic diversity and in groups in which the individuals were presented with equal nutritional opportunity. These qualifications are implicit throughout this paper unless otherwise stated.

(*a*) *General Flock*

The Roseworthy College flock on which the observations were made is of pure South Australian (Bungaree) Merino strain. Lambing occurred during the last 2 weeks of April and early May. Lambs were shorn in late August, weaned in September, and shorn again as hoggets 12 months later. All fleeces were weighed at shearing and a midside sample (150-300 g) taken for determination of clean scoured yield. Animals were weighed within 2 weeks of shearing being completed. The parentage of all animals was recorded.

The animals in each group comprised all those surviving for which complete data were available. The number of animals with incomplete records was less than 1 per cent. of the total. The numbers of animals in the various groups and the years of observation are given in Table 1.

For several years (groups 1-4) midside wool samples were taken in late June with a 1-in. calliper in order to determine the amount of wool produced from a unit area of skin. These samples were subsequently scoured and the weight of clean dry wool determined, except for groups 1 and 2, in which the samples were analysed by the method of Daly and Carter (1954). There is no information on the errors associated with this method of sampling for the determination of unit area production. It seems likely, however, that the most serious errors will be those associated with stretching or compression of the skin, according to the

manner in which the animal is lifted and laid on the standard sampling table. Every effort was made to reduce errors from this source as much as possible by the adoption of consistent methods in the handling and restraint of the animals during sampling.

The measure of weight used in these observations was the mean of the weaning and hogget body weights, i.e. the mean of the weights at the beginning and at the end of the period during which the fleece was produced.

TABLE 1

NUMBERS OF ANIMALS AND YEARS OF OBSERVATIONS

Group	Birth Year	Number Examined			Hogget Shearing Date
		Rams	Ewes	Wethers	
1	1946	—	46	—	Sept. 1947
2	1948	62	122	54	Aug. 1949
3	1949	74	196	118	Aug. 1950
4	1950	61	167	104	Aug. 1951
5	1951	53	173	115	Aug. 1952
6	1952	175	160	—	Aug. 1953
7	1953	—	179	—	Aug. 1954

(*b*) *Group* 8

The group comprised 11 ewes and 13 wethers born between April 16 and 19, 1951. On May 17, 1951, an area 3 by 3 cm was tattooed on the left midside of each animal. At 4 months of age the tattoo area of each animal was closely clipped with small animal clippers and measured. Thereafter, the wool growth from the tattooed areas was harvested at intervals varying from 116 to 130 days for a period of 2 years. The dimensions of the tattoo patch were measured at each sampling and the animals weighed. The raw wool clipped from each sheep was fractionated into clean dry wool, wax, suint, and dirt by the method described by Daly and Carter (1954). Throughout the period of the observations, from August 16, 1951, to August 24, 1953, the sheep were run under field conditions of good husbandry. Wool growth was corrected to a standard period of 120 days.

(*c*) *Statistical Methods*

Covariance and regression analyses formed the greater proportion of analyses on these observations. These have taken the standard form (Fisher 1950). However, for the purpose of testing differences between regression slopes and adjusted means of various classes a modified covariance analysis has been adopted. The pattern of the analysis is set out in Table 2.

For testing the significance between "adjusted means" in normal covariance analysis, the ratio tested is:

$$(C_{yym} - b_0 C_{xy0} + b_c C_{xyc}) / (C_{yyc} - b_c C_{xyc})$$

with $k - 1$ and $n - k - 1$ degrees of freedom. The numerator is the sum of lines 2 and 3 of the analysis of variance in Table 2, while the denominator is the sum of lines 4 and 5; each with its appropriate degrees of freedom. This has the obvious disadvantage that different sources of variation are pooled; this is likely to be important when line 4 is significant. However, in the present observations the contribution of line 4 to the residual term was small, and did not affect the outcome of the analyses in any instance.

TABLE 2

SUMS OF SQUARES AND CROSS-PRODUCTS

Class	Subscript	Sx^2	Sxy	Sy^2	b
General	t	C_{xxt}	C_{xyt}	C_{yyt}	b_t
Class					
1	1	C_{xx1}	C_{xy1}	C_{yy1}	b_1
•	•	•	•	•	•
•	•	•	•	•	•
•	•	•	•	•	•
k	k	C_{xxk}	C_{xyk}	C_{yyk}	b_k
Total within groups	c	C_{xxc}	C_{xyc}	C_{yyc}	(b_c)*
Between groups	m	C_{xxm}	C_{xym}	C_{yym}	b_m
Total	0	C_{xx0}	C_{xy0}	C_{yy0}	(b_0)

Analysis of Variance

Source	D.F.	S.S.
(1) Overall slope	1	$b_0 C_{xy0}$
(2) Slope of means *v.* slope within groups	1	$b_c C_{xyc} + b_m C_{xym} - b_0 C_{xy0}$
(3) Scatter of group means about regression of means	$k - 2$	$C_{yym} - b_m C_{xym}$
(4) Between slopes of group regressions	$k - 1$	$\sum_{i=1}^{k} b_i C_{xyi} - b_c C_{xyc}$
(5) About regression within groups (residual)	$N - 2k$	$C_{yyc} - \sum_{i=1}^{k} b_i C_{xyi}$
(6) Total	$N - 1$	C_{yy0}

* Brackets indicate that the quantities are obtained from the corresponding line and are not the sums of the columns above them.

III. RESULTS

(*a*) *Body Weight and Wool per Unit Area*

The correlation coefficients between log body weight and log wool production per sq. in. are given in Table 3. Only one coefficient (group 3

ewes) was significant and there was no consistency with respect to sign; positive and negative correlations were observed in approximately equal proportions. There was reasonable evidence from this examination therefore that, under the conditions of husbandry operating, body weight and wool production per unit area of midside body surface were independent. On the other hand, there was a highly significant correlation in each group between log fleece weight and log wool per sq. in. (Table 3).

TABLE 3
CORRELATIONS OF LOG WOOL PER SQ. IN. (x_2) WITH LOG BODY WEIGHT (x_1) AND LOG FLEECE WEIGHT (y)

	Group	Number	Correlation Coeff. (r) of	
			x_1 and x_2	x_2 and y
2	Rams	62	− 0.161 N.S.	+ 0.452***
	Ewes	122	− 0.107 N.S.	+ 0.304**
	Wethers	54	+ 0.263 N.S.	+ 0.624***
3	Rams	74	+ 0.076 N.S.	+ 0.655***
	Ewes	196	+ 0.280**	+ 0.621***
	Wethers	118	+ 0.050 N.S.	+ 0.529***
4	Rams	59	− 0.036 N.S.	+ 0.541***
	Ewes	166	− 0.124 N.S.	+ 0.492***
	Wethers	104	− 0.008 N.S.	+ 0.307**
5	Ewes	46	− 0.093 N.S.	+ 0.439**

** $P < 0.01$. *** $P < 0.001$. N.S., not significant.

(*b*) *Regression of Log Fleece Weight on Log Body Weight*

(i) *Sex Differences.*—Figure 1 shows the regression lines fitted to each year-sex group. These have been drawn to cover the weight range observed within the groups. The lower fleece weights of group 2 ewes and wethers and of all group 3 sheep are obvious. This was due to the relatively unfavourable seasons (group 2, 1949; group 3, 1950) during the period of fleece growth. Group 2 rams were not subject to such severe environmental conditions as were the ewes and wethers in the same year because the rams received more favoured treatment in management and grazing. Seasonal conditions were much more favourable in other years and the effect on the grouping of the regression lines is apparent.

The results of the analyses of variance for differences between the sexes in the means and regression slopes are given in Table 4. For year groups 2-5, these analyses have been carried out both including and excluding rams. This was done because rams were removed from the flock and run separately from the ewes and wethers from weaning time. Any difference between rams on the one hand and ewes and wethers on the other therefore includes an environmental component in addition to any real sex difference.

The following are the main points from this analysis:

(1) There was a highly significant regression of log fleece weight on log body weight in all cases.

(2) There was little to suggest a real difference between the sexes in the slopes of the regression lines. The only case in which the "between slopes of group regressions" was significant was in group 2 (ewes *v.* wethers), and in this case significance was only attained at the 5 per cent. level. In the light of the evidence from other groups this is believed to be fortuitous.

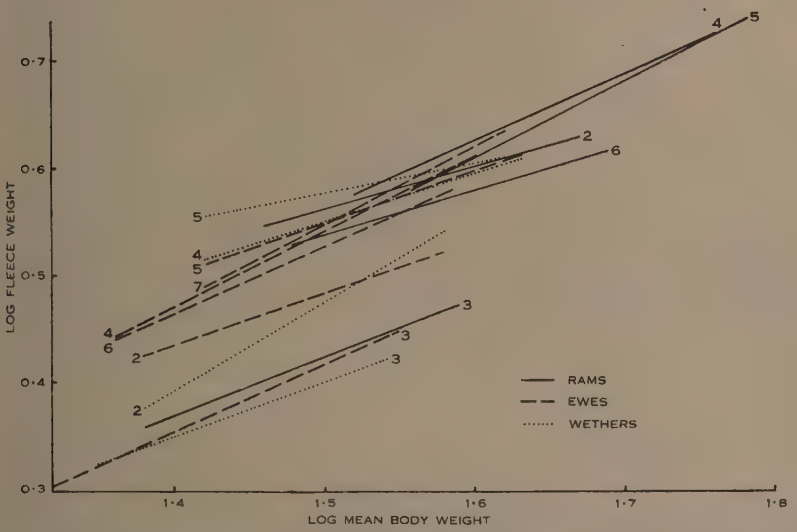

Fig. 1.—Regression lines relating log mean body weight (kg) and log clean fleece weight (kg) in year and sex classes. "Mean" body weight = mean of weaning and hogget weights. Year group indicated by numeral adjacent to regression line. The lines cover the ranges of weight in each group.

(3) The differences between the slopes of the regression line through the sex means and that estimated on a within-sex basis were inconsistent (Table 4, line 2). When ewes and wethers only were considered, the slope of the means was different from the within group slope in group 5 only. When rams also were included, group 5 failed to show significance but two other groups (2 and 4) did so. Similarly with the scatter of sex means around the regression of group of means (Table 4, line 3) only two groups (2 and 5) showed significance in this respect. The inconsistencies observed probably reflect sampling variations and suggest that there is little real difference in wool production between sexes after allowance is made for differences in body weight.

(ii) *Sire Group Differences.*—The data have also been analysed to determine whether progeny groups differed in wool production after

TABLE 4

ANALYSIS OF VARIANCE: REGRESSION OF LOG FLEECE WEIGHT ON LOG BODY WEIGHT; SEX CLASSES

Sex classes: R, rams; E, ewes; W, wethers

Year:	Group 2				Group 3				Group 4			
Sex Classes:	R, E, W		E, W		R, E, W		E, W		R, E, W		E, W	
	D.F.	M.S.	D.F.	M.S.	D.F.	M.S.	D.F.	M.S.	D.F.	M.S.	D.F.	M.S.
(1) Overall slope	1	0.8392***	1	0.1568***	1	0.5102***	1	0.2529***	1	0.7297***	1	0.2796***
(2) Slope of sex means *v.* within group slope	1	0.0977***	1	0.0079	1	0.0034	1	0.0073	1	0.0109*	1	0.0009
(3) About regression of sex means	1	0.0278***	—	—	1	0.0117	—	—	1	0.0007	—	—
(4) Between slopes of sex regressions	2	0.0087	1	0.0115*	2	0.0040	1	0.0076	2	0.0042	1	0.0084
(5) About regression within groups	232	0.0030	172	0.0029	382	0.0032	310	0.0031	326	0.0024	267	0.0024

	Group 5				Group 6		Group 7	
	R, E, W		E, W		R, E		E	
	D.F.	M.S.	D.F.	M.S.	D.F.	M.S.	D.F.	M.S.
(1) Overall slope	1	0.5855***	1	0.1260***	1	0.4116***	1	0.1527***
(2) Slope of sex means *v.* within group slope	1	0.0154	1	0.0493***	1	0.0000		
(3) About regression of sex means	1	0.0397**	—	—	—	—		
(4) Between slopes of sex regressions	2	0.0068	1	0.0069	1	0.0083		
(5) About regression within groups	335	0.0042	284	0.0042	331	0.0032	177	0.0030

* $P < 0.05$. ** $P < 0.01$. *** $P < 0.001$.

correction for weight differences. Because of the suggestion (Table 4) that rams tended to introduce heterogeneity into the data, such progeny have been rejected from this analysis. In group 2, ewes only were considered because of the difference in regression slopes of ewes and wethers, while in group 5, ewes only were considered because of the difference between ewes and wethers in wool production even after adjustment for differences in body weight. In groups 3 and 4, the data from ewes and wethers were combined by pooling variances and covariances calculated within sex.

The results of the regression analyses for differences between sire groups are given in Table 5. The following are the main features of the analyses:

(1) The overall regression of log fleece weight on log body weight was highly significant in all cases.

(2) There were no differences between the sire groups in the slopes of the regression lines.

(3) There was significant scatter of sire group means about the regression of group means in all cases except group 5 ewes, while in two years (group 3 and group 6 rams) the slope of the regression of the means differed significantly from the within group slope. These indicate that there was a highly significant difference between sire groups in log fleece weight after correction for log body weight.

Table 6 shows the regression coefficients of log fleece weight on log body weight observed in the various year and sex groups. In addition to estimating the coefficients from the total variances and covariances for each of the main year and sex classes, coefficients have also been calculated on a "within sire" basis. These latter are included in Table 6. The mean values of the regression coefficients for the sexes, obtained by pooling variances and covariances within year and sire subclasses, were:

Rams	$b = 0.52 \pm 0.056$,
Ewes	$b = 0.61 \pm 0.038$,
Wethers	$b = 0.50 \pm 0.068$.

In normal regression methods it is assumed that the independent variate—log body weight here—is measured without error. Yates (1939) has drawn attention to the fact that where errors are present in the independent variate, the ordinary tests of significance are only valid when differences from zero are being tested. When errors are present, some bias may be introduced which generally reduces the value of the estimated regression coefficient. We have no means of assessing the magnitude of the errors in the measurement of body weight in these observations, although such errors will be small compared with the biological variation. It seems likely, however, that the regression coefficients estimated here will be low rather than high.

TABLE 5

MEAN SQUARES FROM ANALYSIS OF VARIANCE: REGRESSION OF LOG FLEECE WEIGHT ON LOG BODY WEIGHT; SIRE GROUPS

Sex classes: R, rams; E, ewes; W, wethers

Group:	2 (E)		3 (E, W)		4 (E, W)		5 (E)		6 (R)		6 (E)		7 (E)	
	D.F.	M.S.	D.F.	M.S.	D.F.	M.S.	D.F.	M.S.	D.F.	M.S.	D.F.	M.S.	D.F.	M.S.
(1) Overall slope	1	0.0779***	1	0.2599***	1	0.2224***	1	0.0897***	1	0.0859***	1	0.1282***	1	0.1527***
(2) Slope of sire group means *v.* within group slope	1	0.0061	1	0.0179*	1	0.0024	1	0.0012	1	0.0176*	1	0.0048	1	0.0008
(3) About regression of sire group means	5	0.0098**	14	0.0111**	8	0.0075**	8	0.0076	9	0.0095**	9	0.0096**	9	0.0095***
(4) Between slopes of sire group regressions	6	0.0042	15	0.0036	9	0.0046	9	0.0035	10	0.0032	10	0.0036	10	0.0043
(5) About regression within groups	108	0.0023	254	0.0029	234	0.0024	153	0.0040	153	0.0031	138	0.0024	157	0.0025

* $P < 0.05$. ** $P < 0.01$. *** $P < 0.001$.

As no experimental determinations were made of the regression coefficients relating log surface area to log body weight in these animals, it was necessary to compare the above estimates with values determined in other observations or with empirical expectations. In bodies of uniform shape and constant specific gravity, the empirical value of the regression coefficient in area-weight relationships is 0.67. The most extensive experimental observations of area-weight relationships in sheep are those of Ritzman and Colovos (1930), who found values in Southdown × Rambouillet sheep of 0.501, 0.520, and 0.556 in 23 lambs, 32 yearlings, and

TABLE 6

REGRESSION COEFFICIENTS OF LOG FLEECE WEIGHT ON LOG BODY WEIGHT

Group	Rams	Ewes	Wethers
Total			
2	0.39 ± 0.132	0.49 ± 0.092	0.83 ± 0.147
3	0.54 ± 0.122	0.63 ± 0.079	0.51 ± 0.108
4	0.63 ± 0.128	0.70 ± 0.081	0.45 ± 0.108
5	0.71 ± 0.239	0.49 ± 0.104	0.27 ± 0.131
6	0.42 ± 0.084	0.62 ± 0.094	—
7	—	0.72 ± 0.101	—
Within sires			
2	0.53 ± 0.123	0.53 ± 0.091	0.87 ± 0.158
3	0.60 ± 0.138	0.55 ± 0.078	0.57 ± 0.113
4	0.66 ± 0.110	0.72 ± 0.082	0.47 ± 0.116
5	0.70 ± 0.261	0.52 ± 0.115	0.32 ± 0.142
6	0.49 ± 0.084	0.68 ± 0.097	—
7	—	0.71 ± 0.098	—
Mean (within year and sire)	0.52 ± 0.056	0.61 ± 0.038	0.50 ± 0.068

60 adults respectively. Lines and Peirce (1931) found a value of 0.59 in the same strain of Merino sheep as those on which the present observations were based. Brody (1945) records a value of 0.57 in Shropshire sheep, while values observed in cattle do not differ greatly from these: beef cattle, 0.56 (Brody, Comfort, and Matthews 1928); dairy cattle, 0.56 (Elting 1926), 0.60 (Brody, Comfort, and Matthews 1928).

In two limited series of observations on the expansion accompanying body growth of skin areas tattooed on animals during early life, the results given in Table 7 were obtained. All the areas measured were situated on the trunk. These values will certainly be higher than that of the whole skin because of the lateness of the development of the trunk relative to that of the head, neck, and legs (Hammond 1932; McMeekan 1940). However, caution is needed in comparing these latter coefficients with the fleece-weight–body-weight regression coefficients considered here. This is because the present fleece-weight–body-weight comparison was made on different animals at the same age (type B, Richards and Kavanagh

1945), while the tattoo-area–body-weight relationships were made on the same animals at different ages (type C, Richards and Kavanagh 1945). It is probable that different values would be obtained from the two methods, as Brody (1945) has shown in humans; the former giving lower values because of changes in form and specific gravity.

TABLE 7
REGRESSION OF LOG TATTOO AREA ON LOG BODY WEIGHT

Group	No.	Region of Body	Duration of Observations	*b*
Series 1	24	Midside	1 month to 23 months of age	0.71
Series 2	8	Mid back	Birth to 4 months	0.78
	8	Shoulder	Birth to 4 months	0.62
	8	Midside	Birth to 4 months	0.88
	8	Thigh	Birth to 4 months	0.64
	8	Mean of above 4 (within sheep and region)	Birth to 4 months	0.73

Accurate estimates of skin area and its relation to body weight are clearly necessary. However, for our immediate purpose a regression coefficient of 0.60 appears a reasonable one to adopt. None of the individual regression coefficients calculated within year and sire classes (lower half of Table 6) differs significantly from 0.60, and only one (group 5 wethers) differs significantly from 0.65.

(*c*) *Relation of Fleece Weight to Body Weight and Wool per Unit Area*

The multiple correlation coefficients relating log fleece weight to log body weight and log wool per sq. in. are given in Table 8. If all measures were made without error and log body weight was an accurate index of wool-bearing surface, then the multiple correlation coefficient would be unity. The values observed varied from 0.49 to 0.78. Accurate determination of where the errors occurred in these data is not possible but they are believed to have arisen largely in the measurement of wool production per unit area. Simple and partial regression coefficients of log fleece weight on log body weight are also included in the table. There is good agreement between the corresponding simple and partial coefficients, as is to be expected from the low correlation between the two independent variates (log body weight and log wool per sq. in.) recorded in Table 3.

(*d*) *Group* 8

The means and the regression lines relating wool production to tattoo area for each of the six periods in these observations are given in Figure 2.

The tattoo areas used in the regression analysis are the means of the areas at the beginning and at the end of each period. For clarity, the individual points are omitted. The periods clearly fall into two groups: an upper group comprising periods 1, 3, and 4 and a lower group of periods 2, 5, and 6. This grouping closely reflects seasonal conditions and pasture feed supply during the periods. Periods 1 and 4 occurred in spring and early summer, when pasture feed supplies were good; periods 2 and 5

TABLE 8

MULTIPLE CORRELATION, AND SIMPLE AND PARTIAL REGRESSION COEFFICIENTS, OF LOG FLEECE WEIGHT (y) ON LOG BODY WEIGHT (x_1) AND LOG WOOL PER SQ. IN. (x_2)

Group		N	R	Indep. Variate	Simple b	Partial b
2	Rams	62	0.62	x_1	0.39 ± 0.132	0.48 ± 0.113
				x_2	0.37 ± 0.094	0.42 ± 0.084
	Ewes	122	0.53	x_1	0.49 ± 0.092	0.53 ± 0.085
				x_2	0.24 ± 0.068	0.28 ± 0.060
	Wethers	54	0.78	x_1	0.83 ± 0.147	0.65 ± 0.122
				x_2	0.57 ± 0.099	0.45 ± 0.082
3	Rams	74	0.78	x_1	0.54 ± 0.122	0.48 ± 0.088
				x_2	0.59 ± 0.080	0.56 ± 0.067
	Ewes	196	0.71	x_1	0.63 ± 0.079	0.45 ± 0.067
				x_2	0.54 ± 0.049	0.46 ± 0.046
	Wethers	118	0.65	x_1	0.51 ± 0.108	0.48 ± 0.091
				x_2	0.40 ± 0.060	0.39 ± 0.054
4	Rams	59	0.77	x_1	0.63 ± 0.128	0.64 ± 0.099
				x_2	0.45 ± 0.092	0.46 ± 0.070
	Ewes	166	0.70	x_1	0.70 ± 0.081	0.64 ± 0.070
				x_2	0.46 ± 0.063	0.40 ± 0.052
	Wethers	104	0.49	x_1	0.45 ± 0.108	0.45 ± 0.102
				x_2	0.24 ± 0.073	0.24 ± 0.067
1	Ewes	46	0.63	x_1	0.60 ± 0.201	0.66 ± 0.174
				x_2	0.38 ± 0.118	0.42 ± 0.104

covered late summer and autumn, when feed supplies were at a minimum; periods 3 and 6 occurred in winter, when feed conditions depended largely on the occurrence of opening rains. In period 3 (winter 1952) opening rains occurred early (April) and excellent grazing was available throughout the period. In the following year, the winter (period 6) was below average owing to the lateness of the opening rains (June) and poor feed growth throughout the period. The seasonal trends in mean wool production per tattoo area, in mean wool production per unit area, and in mean tattoo area are illustrated in Figure 3. Because of the difference in mean wool production, subsequent statistical analyses were carried out

separately on periods 1, 3, and 4 (favourable periods), and periods 2, 5, and 6 (unfavourable periods).

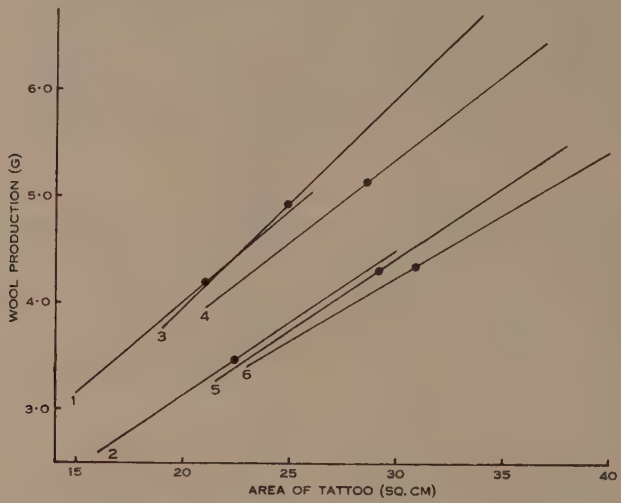

Fig. 2.—Regression lines relating wool production to area in six 4-monthly periods (group 8). The group mean is indicated on each line. The lines cover the range of tattoo areas observed in each period.

The data were examined for differences in wool production between sheep and between periods, by analysis of covariance in a randomized

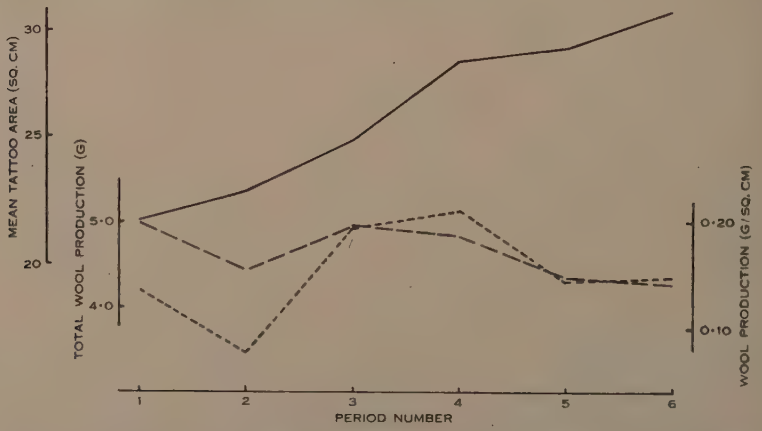

Fig. 3.—Trends for 24 animals in mean tattoo area (continuous line), wool production per tattoo area (short dash line), and wool production per unit area (long dash line) during six consecutive 4-monthly periods (group 8). "Mean" tattoo area = mean area at beginning and end of period.

block as described by Wishart (1950). The results of these analyses are given in Table 9. In both favourable and unfavourable seasons there was

a highly significant difference between sheep in wool production after "adjustment" for differences in tattoo area. The repeatability of wool production per unit area, calculated as the sheep intraclass correlation, was 0.68. There was also a highly significant difference between periods 1, 3, and 4 in "adjusted" wool production, but not between periods 2, 5, and 6, although these are of no importance in the present consideration.

TABLE 9

ERRORS OF ESTIMATES FROM ANALYSIS OF COVARIANCE

Source	D.F.	M.S.
Periods 1, 3, *and* 4		
Sheep	23	1.6885***
Periods	2	1.3856***
Error	45	0.1412
Periods 2, 5, *and* 6		
Sheep	23	1.0676***
Periods	2	0.0847 N.S.
Error	45	0.1197

*** $P < 0.001$. N.S., not significant.

The regression lines for each period were examined for passage through the origin using the method described by Mather (1949). In no case was there a significant departure. Each period regression line was also examined for departure from linearity by fitting a quadratic term. The results are given in Table 10: in no case was a significant departure from linearity observed.

TABLE 10

ANALYSIS OF VARIANCE: REGRESSION OF WOOL PRODUCTION ON TATTOO AREAS

Source	D.F.	Mean Squares for Periods					
		1	2	3	4	5	6
Regression:							
Linear	1	4.9271***	4.4897***	9.5408***	7.4911***	7.4651***	11.289***
Quadratic	1	0.8516	0.0109	0.0723	0.6736	0.1357	0.003
Deviations	21	0.6252	0.4278	0.5403	0.8997	0.4310	0.5561

*** $P < 0.001$.

IV. DISCUSSION

The absence of a consistent correlation, either positive or negative, between clean wool produced per sq. in. of midside body surface and body weight indicates biological independence of these two characters in this flock of sheep. There was nothing to suggest that large sheep tended to produce either more or less wool per unit area when all sheep were subject

to similar treatment. This observation is in agreement with those of Morley, Lockart, and Davis (1955), who recorded non-significant correlation coefficients of −0.13 and −0.04 in rams and ewes respectively, between body weight at 18 months and raw fleece production per unit area of midside skin. In the present observations there was a highly significant correlation (Table 3) between clean fleece weight and wool production per unit area of midside body surface. Morley, Lockart, and Davis (1955) also found a highly significant correlation between greasy fleece weight and raw wool production per unit area.

If unit area wool production is unrelated to body weight but significantly related to total fleece production, as these observations suggest, then it follows that total clean fleece production is a function of wool-bearing area and unit area production. No measures of surface area were made in these sheep, and it was necessary therefore to approach the problem indirectly by means of the regression of log fleece weight on log body weight. Agreement between this regression coefficient and that of log surface area on log body weight (approximately 0.60) was interpreted as indicating a direct relationship between surface area and clean wool production.

Of the 15 regression coefficients calculated in the various groups, not one was significantly different from 0.60 and only one was significantly different from 0.65. In view of the numbers of sheep involved and the variety of seasons covered during the period of the observations, considerable confidence is placed on these coefficients.

The observations of wool production in early adult life on areas of skin defined on the young lamb supply confirmatory evidence of the relationship of fleece production to body weight and skin area. As the tattoo areas on each animal were the same when animals were 1 month of age, differences present at later ages, when wool production was measured, were the result of differences between individual animals in growth after 1 month. The important features of the statistical examination of the data are, firstly, linearity of the regression of wool production on tattoo area, and secondly, passage of the regression lines through the origin. These features were observed in each of the periods considered, despite the variations in wool production between periods owing to grazing conditions.

In summary, the three main results were: (i) zero correlation between body weight and unit area midside wool production; (ii) a regression coefficient of log fleece weight on log body weight similar to that relating log surface area to log body weight; (iii) a linear relationship of wool production to the area of midside tattooed patches. These results clearly establish that under the conditions of the present observations, fleece weight was proportional to estimated smooth body area.

The results reported, with respect to linearity of the relationship of wool production to skin area, are in complete agreement with those of

Galpin (1947). In another important respect, however, they disagree. Galpin found no evidence of a significant difference between sheep in wool production per unit area of skin. In the results recorded here there was a highly significant difference between sheep. Further, Marston (1948) has shown differences between sheep, in wool production per unit area under identical nutritional treatment, amounting to a factor of 2.0. Galpin emphasizes that constancy of unit area wool production is only attained under conditions where nutritional conditions are not limiting. In so far as it is possible ever to meet such a condition, it seems unlikely that Marston's sheep fed at twice maintenance suffered nutritional limitation. The results of Ferguson, Carter, and Hardy (1949) also are not in agreement with a concept of constant wool production per unit area of skin. The disagreement between Galpin's (1947) results and those recorded here might be the result of the different breeds examined, but are believed more likely to result from the fact that Galpin's observations were based on only six sheep at three periods, whereas the present observations are based on 24 animals at six periods. The "constancy" of wool production per unit area of skin in a particular region which was suggested by Galpin appears unlikely on general genetic grounds. At best it can be only approximately correct, as suggested by Henderson (1953). The problem would appear to resolve itself into what, if any, variance can be associated with a "constant".

The significant differences observed between sire groups in mean wool production, after correction for differences in body weight, are further evidence that wool production per unit area of skin is not constant, and further, that at least a portion of the variability in this character has a genetic basis. This result provides something of an exception to the generality of the relationship between wool production and body weight recorded above, in the sense that sire groups having the highest mean body weight are not necessarily those that have the highest mean wool production. However, within sire groups the relationship of wool production to body weight was quite consistent, as judged from the fact that the "between slopes of sire group regressions" (Table 5) were non-significant in each year.

Fleece weight is determined by two factors: wool production per unit area, and surface area, or more strictly fleece-bearing surface. These observations indicate that these two factors are independent (Table 3). Morley (1955) found no significant genetic correlation between body weight and fleece weight. This implies that these characters are genetically independent, and therefore that the phenotypic association of fleece weight with body weight is of environmental and not of genetic origin.

The significant differences between sire groups in wool production, after correction for differences in body weight, indicate that there is genetic variation in unit area wool production, while Morley (1955) and Hazel and Terrill (1945, 1946) have observed genetic variability in body

size. It is reasonable to suggest therefore that selection for improved fleece weight should involve consideration of both these characters. As maintenance energy requirements are approximately related to skin area, attention to unit area production might well have the added advantage of indirect selection for sheep which are more efficient economically. However, no conclusions can be reached on this point until the relationship of wool production to feed intake is more clearly defined. Also, if the correlation between fleece weight and body weight is of environmental origin, then estimates of heritability of wool production corrected for differences in body weight may be substantially improved, using the method developed by Rendel (1954) from the earlier studies of Fairfield Smith (1937) and Hazel (1943).

In view of the fact that unit area wool production is a determinant of fleece weight, we suggest that this character should be the subject of increasing attention in biological work, rather than fleece weight itself. We have frequently observed in this flock that twins have the same unit area wool production as singles but, owing to the early post-natal check of twins, their follicle number per unit area is reduced (Schinckel 1955). The twins compensate for the reduced follicle number by producing a longer and thicker fibre. Also, the experimental evidence of Henderson (1953) and Short (1955) leads to the conclusion that unit area wool production is independent of follicle number within the breeds examined. Developmentally, fibre length and diameter must therefore be regarded as results of unit area wool production and follicle number.

This raises the interesting problem of the causes of differences between sheep in unit area productivity. If the above concepts are correct, production is unrelated (causally) to the metrical characters—fibre number and fibre size. Physiologically the differences must result either from differences between animals in the efficiency with which material (substrate) presented to the follicle is converted to fibre keratin, or in the amount of this substrate, or from both these factors.

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FLEECE GROWTH OF YOUNG LINCOLN, CORRIEDALE, POLWARTH, AND FINE MERINO MAIDEN EWES GRAZED ON AN UNIMPROVED PASPALUM PASTURE

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Summary

Two young maiden ewes of each of the Lincoln, Corriedale, Polwarth, and fine Merino breeds were kept together on 3 acres of unimproved paspalum-dominant pasture at Castle Hill, near Sydney, for 42 weeks. In this time 44½ in. of rain were recorded, with fairly uniform monthly incidence. The response of the sheep to these conditions was studied and compared with that of similar sheep which were kept in housed, single pens and fed unrestricted quantities of a high-quality diet (Daly and Carter 1955).‡

Liveweight and wool production of the field sheep were dependent on seasonal trends in pasture quality and were consistently lower than for the housed, well-fed sheep.

Rain removed appreciable quantities of wax and suint from the fleeces of Lincolns, Corriedales, and Polwarths and altered the pattern of distribution of these components in them. In warm, wet conditions "canary stain" and bacterial discoloration became conspicuous in Corriedale and Polwarth fleeces but not in Lincoln and fine Merino fleeces. In all respects the fine Merino fleeces were least affected by the relatively severe climatic conditions.

I. INTRODUCTION

Daly and Carter (1955) have reported an experiment on fleece growth (experiment I of that paper) in which four yearling maiden ewes of each of the breeds Lincoln, Corriedale, Polwarth, and fine Merino, were kept in single pens in a sheep-house on unrestricted quantities of a palatable diet of 21 per cent. crude protein content. While that experiment was being conducted, another (experiment III) was undertaken collaterally with two ewes of each breed which were run together on an unimproved pasture. The purpose of this latter experiment was to make breed comparisons under another set of conditions, and data so obtained are presented in this paper.

II. METHODS

The plan and time schedule of experiment III are shown in Figure 1. The eight sheep were grazed on a 3-acre paddock at Castle Hill, near

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‡ DALY, R. A., and CARTER, H. B. (1955).—*Aust. J. Agric. Res.* **6**: 476.

Sydney. *Paspalum dilatatum* Poir. dominated the pasture, though useful forage was provided in the spring by some brome grasses and volunteer legumes. At no time was the quantity of forage available an obviously limiting factor; the quality, however, deteriorated after the paspalum had seeded in late December and this deterioration was accentuated towards the end of the experiment by the fairly warm and wet conditions which then existed (see Fig. 2).

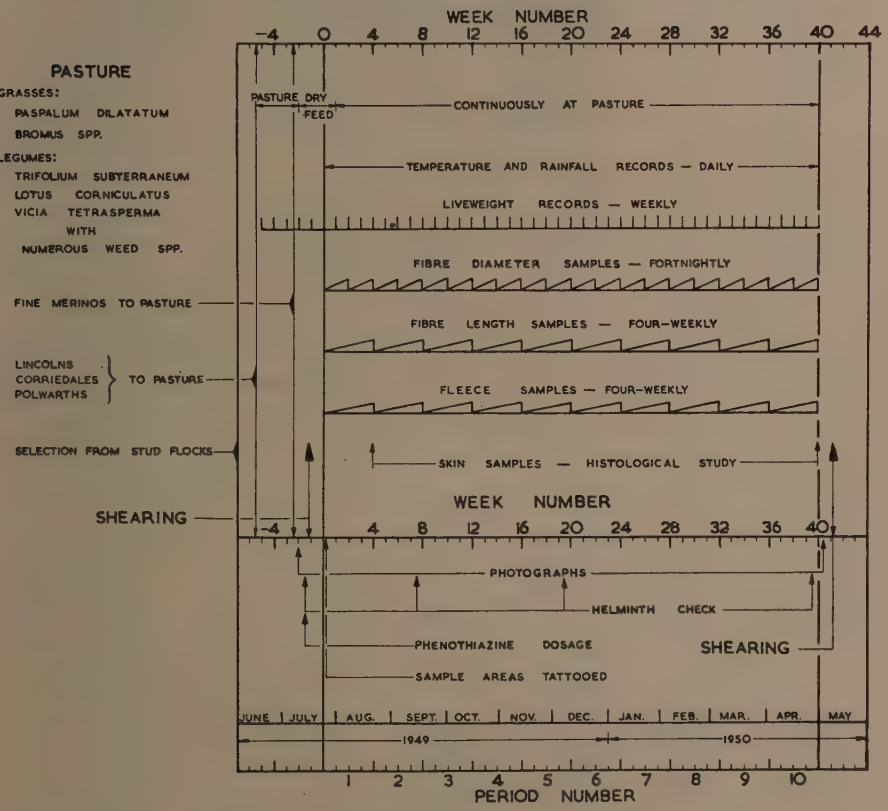

Fig. 1.—The plan and observation time schedule of experiment III.

Where practicable the experimental techniques of experiment I were employed. An estimate of the weight of wool produced in each period by each sheep was made by apportioning the weight of clean wool in the fleece shorn at the conclusion of the experiment to the various periods on the basis of the observed weights produced on the right midside patch. No comparable estimates for wax and suint production could be obtained, as the moderately heavy falls of rain in almost every period caused appreciable quantities of these components to be removed from the fleece.

III. Results

The trend in liveweight in the later periods (Fig. 2), gives a fair indication of the decline in the quality of the pasture in the latter half of experiment III. As in experiment I the breeds showed clear differences in the liveweight attained, and the relative weights were of the same order though at lower absolute levels.

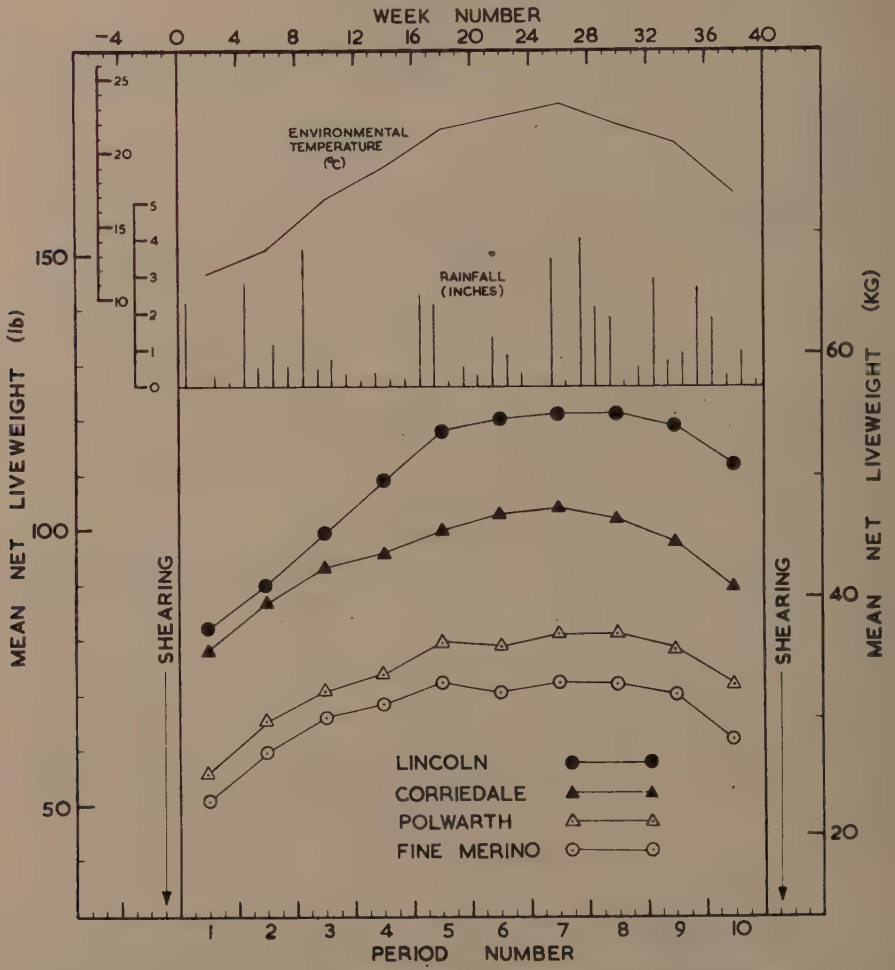

Fig. 2.—The mean 4-weekly net liveweight of the sheep in experiment III.

Measurements of the follicle population gave results which agreed generally with those of experiment I (Table 1), though here the follicle densities were higher and the fibre diameters lower (fine Merinos excepted). One of the Merinos was exceptional in that its n_s/n_p ratio was

41.8 at period 1 and 44.6 at period 10, values unusually high and representing the upper limits so far observed in the breed; this animal had a primary density of about half that of other fine Merinos.

TABLE 1

CHARACTERS OF THE FOLLICLE POPULATION AT PERIODS 1 AND 10 OF EXPERIMENT III

Character	Period	Lincoln	Corriedale	Polwarth	Fine Merino
Total follicle density (n_{s+p}/sq. mm)	1	21.6	35.4	80.7	110.5
	10	13.7	29.7	58.7	93.9
Primary follicle density (n_p/sq. mm)	1	3.1	3.1	4.8	3.9
	10	2.4	3.0	4.1	3.1
Ratio n_s/n_p	1	5.9	10.3	15.6	30.7
	10	4.6	9.0	14.9	33.2
Diameter primary fibres, $\bar{d}_p$ (μ)	1	54.5	30.0	27.1	22.1
	10	53.1	27.6	27.0	20.6
Diameter secondary fibres, $\bar{d}_s$ (μ)	1	36.5	30.8	24.0	19.7
	10	42.8	27.6	22.8	17.9
Ratio $\bar{d}_p/\bar{d}_s$	1	1.38	0.97	1.13	1.12
	10	1.24	1.00	1.18	1.15

Differences between the breeds in fibre growth were clear-cut (Tables 2 and 3). A smaller weight of wool—of the order of 70 per cent. as much—was produced by the field sheep than by the well-fed, housed sheep

TABLE 2

MEAN VALUES OF CHARACTERS FOR PERFORMANCE OVER PERIODS 2-10 OF EXPERIMENT III*

Character	Lincoln	Corriedale	Polwarth	Fine Merino
Net liveweight (lb)	112.5 (1.64)	97.1 (1.42)	76.0 (1.11)	68.4
Fibre cross-sectional area (μ^2)	1234 (4.11)	742 (2.47)	471 (1.57)	300
Fibre length (mm/28 days)	18.5 (2.03)	14.6 (1.60)	13.0 (1.43)	9.1
Individual fibre volume ($mm^3 \times 10^{-3}$/28 days)	22.89 (8.41)	10.90 (4.01)	6.16 (2.27)	2.72
Clean wool per sheep (g/28 days)	376 (1.93)	277 (1.42)	254 (1.30)	195

* Values in brackets are breed means relative to that of the fine Merino = 1.00.

and the fibres produced in the field were of smaller dimensions for all breeds except the fine Merinos. That poor nutrition influences fibre thickness rather than length is seen again, as for the Lincolns, Corriedales,

TABLE 3

GROWTH OF WOOL IN SELECTED PERIODS OF EXPERIMENTS III AND I

Breed	Period	Fibre Cross Section (μ^2)		Fibre Length (mm/28 days)		Individual Fibre Volume ($mm^3 \times 10^{-3}$/28 days)		Wool per Sheep (g/28 days)	
		Expt. III	Expt. I	Expt. III	Expt. I	Expt. III	Expt. I	Expt. III	Expt. I
Lincoln	2	1004	1487	16.6	18.9	16.71	27.97	240	472
	6	1384	1723	18.8	19.5	25.98	33.50	455	621
	10	1058	1527	17.6	20.0	18.68	30.40	309	522
Corriedale	2	745	1036	14.4	15.7	10.74	16.34	229	374
	6	768	1037	15.4	15.6	11.84	16.28	314	452
	10	503	847	12.4	15.0	6.29	12.66	167	357
Polwarth	2	499	678	12.8	13.7	6.43	9.32	243	369
	6	475	619	12.7	14.2	6.04	8.81	257	362
	10	360	517	12.3	14.0	4.46	7.27	185	294
Fine Merino	2	317	353	9.9	9.1	3.18	3.24	166	292
	6	298	311	9.4	9.3	2.78	2.89	222	317
	10	236	238	8.6	8.9	2.00	2.15	137	221

and Polwarths the cross-sectional area of fibres in experiment III was 75-80 per cent. of those produced in experiment I, while the length of fibres produced in the former was 90 per cent. and higher of those in the latter. The similarity of the dimensions of the fibres produced by the fine Merinos in all periods in the field and in the pens was unexpected and no conclusive explanation of this finding can be offered. The overall trends of wool growth in the field approximated to those of smooth curves through ordinates for periods 2, 6, and 10 (Table 3) and, as in experiment I, there was no significant change in fibre length growth through the experiment.

TABLE 4

MEAN WEIGHTS OF SKIN PRODUCTS IN FLEECES SHORN AT COMPLETION OF EXPERIMENTS III AND I*

Breed	Experiment	Wool (kg)	Wax (kg)	Suint (kg)
Lincoln	III (2 sheep)	3.59	0.13	0.17
	I (3 sheep)	4.53	0.62	0.75
Corriedale	III (2 sheep)	2.65	0.32	0.22
	I (1 sheep)	5.07	0.69	0.72
Polwarth	III (2 sheep)	2.50	0.14	0.10
	I (4 sheep)	3.02	0.62	0.50
Fine Merino	III (2 sheep)	1.89	0.49	0.13
	I (4 sheep)	2.39	0.91	0.25

* Growth period in experiment III was 42 weeks; in experiment I it was 40 weeks.

Finally, the data of Table 4 show the overall influence of nutrition on fleece growth and the loss of wax and suint from the fleece through the leaching effect of rainfall. Though some wax was removed from the midside patches in those periods in which rain fell, proportionately more suint was removed from the same area, especially if heavy rain was recorded towards the end of a period. The removal of further quantities of both components from fleece staples other than fine Merino exposed to the weather for all periods, is evidenced by the results of Table 5, as Daly (unpublished data) has observed that where fleeces are protected from rainfall the proportions of fleece components in the sum of monthly clippings from the midside agree closely with those in a continuously grown shoulder staple.

IV. DISCUSSION

Differences between breeds when each is represented by only two sheep must be regarded with due caution. Confidence in the general applicability of the results of the field experiment is increased, however, as the relative positions of the breeds in observed liveweight and wool production were similar to those recorded for experiment I.

In the field the sheep were dependent solely on the pasture in a 3-acre paddock. From observations of that pasture and the trend in liveweight it was apparent that the quality of the pasture improved in the early periods and declined in the later ones especially after period 6. This was essentially a seasonal trend and was accompanied by a similar trend in wool production. As the sheep in the field were not afforded a constant level of nutrition nor one as high as that offered the sheep in the housed pens, wool production in the former was less than in the latter.

TABLE 5

EXPERIMENT III: PROPORTIONS OF SKIN PRODUCTS IN THE SUMMED RIGHT MIDSIDE PATCH SAMPLES FOR PERIODS 1-10 AND IN THE LEFT SHOULDER STAPLES OF THE SAME GROWTH PERIOD

Breed	Sample	Percentage of Total Skin Products		
		Wool	Wax	Suint
Lincoln	Summed patch samples	86.64	8.53	4.42
	Shoulder staple	93.26	3.80	2.94
Corriedale	Summed patch samples	77.06	17.76	5.18
	Shoulder staple	86.59	10.72	2.70
Polwarth	Summed patch samples	83.50	12.10	4.41
	Shoulder staple	91.66	6.18	2.16
Fine Merino	Summed patch samples	74.70	21.87	3.43
	Shoulder staple	73.84	22.01	4.16

During experiment III, 44½ in. of rain were recorded and its incidence was fairly uniform, as period 4 was the only one in which less than 2½ in. fell. The maximum intensity recorded was 3½ in. per day, and on 13 days over 1 in. fell. To these conditions the fleeces displayed distinctive responses. The long, loose, and open fleece of the Lincoln, with its relatively high suint content, is easily penetrated by rain, and drainage from the greater part of the skin surface is also relatively free. By contrast, the compact and closely arranged staples of the fine Merino fleece, with its high wax content, impede the free entry of rain. The Corriedale and Polwarth fleeces clearly occupy successive intermediate positions in these respects, possessing neither the free moisture drainage of the Lincoln nor the resistance to moisture penetration of the fine Merino fleece. The consequences of these differences in fleece structure were seen in the removal of portion of the skin secretions from the fleece, or their translocation from dorsal to more ventral regions or from one part of the staple to another, under the action of rain.

Fleece structure, the content of skin secretions, and the action of rain also render intelligible the incidence and character of fleece discolorations which developed in the persistent warm and wet conditions in about period 8. These discolorations, which were not removed from the wool

fibre by carbon tetrachloride or distilled water, were most prominently developed in the Corriedale and Polwarth staples and less in Lincoln staples, and were not obvious in fine Merino staples. An orange-yellow banded stain developed where an accumulation of suint had occurred through the agency of the rain; these bands were close to the skin surface on dorsal body regions and closer to the tip of the staple on the more ventral parts. A second discoloration, which was green and characteristic of the growth of *Ps. pyocyaneus*, occurred most prominently in the Polwarth fleeces and more strictly on the dorsal body regions. There was some evidence that this latter stain originated on or near the skin surface but eventually became more widely diffuse than the orange stain. By contrast, the Lincoln fleeces were relatively free from discoloration and generally presented a well-washed appearance, while the fine Merino fleeces showed little evidence of the disturbing effect of rain either in the distribution of skin secretions or in the general character of the staple. This being so, the fine Merino merits consideration as being superior to these other breeds in resisting the bad effects of heavy rainfall on the fleece. Our experience of field conditions in high rainfall areas and during exceptionally wet years suggests that the performance of the fine Merino compares at least favourably with that of other types of sheep including other strains of the Merino, and that the range of conditions under which fine Merino wool can be grown satisfactorily is wider than that which is generally accepted.

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